Determinants of Modular Societies in Snub-nosed Monkeys (*Rhinopithecus bieti*) and other Asian Colobines

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For

My wife Carol Jin Grüter

&

My mother Jutta Porr-Gwildies

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“I hear and I forget. I see and I remember. I do and I understand.”
Confucius

Contents

Summary

The fundamental question of socioecology is what determines sociality, or more specifically, what determines the emergence of a particular social system. Primates exhibit a variety of social systems, among which multilevel or modular societies are likely the most complex, the least understood and least investigated. Modular societies are structurally characterized by nuclear one-male units (OMUs) or harems which are habitually embedded within larger relatively coherent social bands. Within the order Primates, modular societies are uncommon, found in only a few species, e.g. hamadryas baboons, gelada baboons, proboscis monkeys, snub-nosed monkeys and humans (multifamily system). In an attempt to elucidate the evolution and functional determinants of modular societies in primates, I chose a twofold approach: First, I conducted a comparative analysis focusing on Asian colobines (Presbytini) which form either autonomous and often territorial uni-male groups (e.g. *Presbytis* spp.) or modular associations (most odd-nosed colobines, i.e. *Nasalis*, *Rhinopithecus*, *Pygathrix*), with the latter encompassing both tight bands composed of OMUs and loose neighborhoods of OMUs. I did a phylogenetic reconstruction of modularity in the Presbytini, revealing that the single OMU pattern is probably the ancestral state while the modular pattern is a derived feature. In order to answer the key question of why OMUs in some colobines have the propensity to congregate, I tested predictions of three socioecological hypotheses by means of general linear models and independent contrasts and evaluated other scenarios descriptively due to difficulties of quantifying them. Odd-nosed monkeys in general and black-and-white snub-nosed monkeys (*Rhinopithecus bieti*) in particular do not seem to accrue obvious ecological benefits from band formation such as thermoregulation, predation avoidance or enhanced efficiency of resource harvest. I found partial support for the bachelor threat hypothesis, i.e. that the number of non-reproductive bachelor males is a significant predictor variable of band formation. The threat posed by 'gangs' of bachelor males is thought to force OMUs to aggregate as a means of decreasing the amount of harassment and the risk of takeovers and infanticide, and thus may represent a salient force shaping the modular sociality. In the odd-nosed colobines and snub-nosed monkeys in particular, phylogenetic inertia may also play a part in explicating the modular nature of their society. I also demonstrated via a comparative analysis that modular species have significantly higher levels of sexual dimorphism in body weight than the non-modular ones, suggesting that living in a modular society intensifies the mating competition among males.

The second objective was to undertake a case study of the modular system of *R. bieti*, a highly endangered colobine whose socioecology has received only scant attention. The study was conducted over 20 months on a free-ranging, semi-habituated band in the montane Samage Forest (Baimaxueshan National Nature Reserve in Yunnan, PRC) at elevations of 2600 - 4000 m. Various parameters were studied in situ: habitat structure and resource availability in time and space, resource use, range use, and group demographics and dynamics. Habitat and range use was studied via GPS/GIS approach. There is a patchwork of vegetation types at Samage, and six major land cover types were distinguished. The band covered a minimum area of 32 km^2 - among the largest home range estimates for any primate. This large home range was probably due to the combined effects of large group size and forest heterogeneity (with seasonally food-rich areas interspersed with less valuable areas). The band's home range was not used uniformly: I found that mixed deciduous broadleaf/conifer forest was used disproportionately to its availability, and other forest assemblages were mostly used in transit. About one third of the grid cells had more location records than expected based on a uniform distribution, viz. a core area, albeit a disjunct one. My observations implicate temporal and spatial availability of food as a determinant of home range use of the study group. Winter, spring and summer home ranges were equally large, ca 18 km^2. The home range decreased markedly in fall (9.3 km^2), probably because the band obtained sufficient food resources (fruit) in a smaller area. The large winter range is best attributed to the exploitation of dispersed clumped patches of mature fruits. Methodologically speaking, I also point to the fact that primate home range sizes can vary tremendously as a consequence of the chosen analytical technique to estimate home range. My findings show that the grid cell method cannot substitute for the minimum convex polygon (MCP) method and vice versa. I thus propose the method of adjusted polygons, whereby unsuitable and never visited areas are clipped out from the polygon, thus producing more proper results.

Feeding ecology was investigated by means of group scans and investigating feeding litter. Resource abundance was estimated by establishing 67 vegetation plots (20 x 20 m) within which a total of 80 tree species in 23 families were recorded. As measured by basal area, the most common plant families are the predominantly evergreen Pinaceae and Fagaceae, making up 69% of the total tree biomass at Samage. The present findings demonstrate that the monkeys have a relatively diversified diet composed of 94 plant species. The animals expressed high selectivity for uncommon angiosperm tree species such as *Acanthopanax evodiaefolius*, *Sorbus* spp. and *Acer* spp.

The focal band was found to consist of 400 individuals, one of the largest groups of wild primates ever recorded. The wide temporal and spatial availability of lichens - their staple fallback food - reduces the ecological costs of grouping, thus allowing for the formation of 'super-groups'. However, such a large group confers costs of increased food competition, particularly with regard to spatially clumped and temporally restricted food items. Several lines of evidence indicate that the animals are subjected to scramble and contest competition: I found a positive correlation between group size and home range size for different populations of *R. bieti*. Additionally, the high selectivity for uncommon seasonal plant food items found in clumped patches creates the potential for contest competition. This is corroborated by observations that the animals occasionally deplete leafy food patches and male aggressive behaviour is correlated with monthly fruit availability. That individuals keep a longer distance from neighboring conspecifics while feeding as opposed to resting is suggestive of within-unit scramble competition.

Even though the band appears to have been unified for the most part, it occasionally fissioned briefly during the day. I also witnessed a medium-term band split and reunion: two 'sub-bands' of several OMUs were once observed travelling separately for several weeks. OMUs are cohesive entities that usually confine themselves to a single tree when resting and thus are spatially and socially isolated from other OMUs, with males almost never sharing the same tree in the presence of females. Large all-male units (AMUs) composed of adult and sub-adult males as well as juveniles tended to follow the family units closely at all times, and there was a tendency for elevated male aggression when AMU members were present. Measuring of proximity among members of different age-sex classes in OMUs revealed that females associated preferentially with males and vice versa (while controlling for the proportional representation of age-sex classes in the population), resulting in a bisexually-bonded society. Contrary to other Asian colobines, which show low levels of social interaction, *R. bieti* are comparatively social, with grooming occupying 7.3% of the time. Social grooming was primarily a female affair, but males also participated in grooming networks to a considerable degree, further demonstrating that males are relatively affiliative and social with females when compared with males of other colobines. The integration of males into the social network of the OMU is thought to help to maintain OMU integrity and cohesion in the midst of a crowded neighborhood with many other units (both non-reproductive and reproductive) being in close proximity. In a cross-species analysis of Asian colobines, the best predictor variable of grooming frequency was substrate use and not group

size, implying that the hygienic function of allogroming may become important when terrestrialism is high.

A side goal of this research project was to elucidate eco-behavioral adaptations of *R. bieti* to a marginal environment. Only a few primate species thrive in temperate regions characterized by relatively low temperature, low rainfall, low species diversity, high elevation and especially an extended season of food scarcity during which they suffer from dietary stress. The dietary strategy of *R. bieti* is one of adjusting intake of plant food items corresponding with changes in the phenology of deciduous trees in the forest. A non-plant food, lichens, featured prominently in the diet throughout the year (annual representation in the diet was about 67%) and became the dominant food item in winter when palatable plant resources were scarce and when there was a severe reduction in dietary diversity. Additional highly sought winter foods were frost-resistant fruits. The snub-nosed monkeys' choice of lichens as a staple fallback food is likely due to their spatiotemporal consistency in occurrence, nutritional and energetic properties and the ease with which they can be harvested. Using lichens is an uncommon strategy among primates and way to mediate effects of seasonal dearth in palatable plant foods and ultimately a key survival strategy. A comparative analysis revealed that other temperate-dwelling primates rely mainly on buds and bark as winter fallback foods. Moreover, I found evidence for seasonal variation in use of elevational zones. The higher abundance of lichens at higher altitudes explains the monkeys' tendency to occupy relatively high altitudes in winter despite the prevailing cold. My analyses support the hypothesis that elevational migration, in this temperate-subtropical forest, is influenced by the temporal fruiting of major food trees and that climate has only a negligible effect on altitude use.

General Introduction

The fundamental question of socioecology is what determines sociality, or more specifically, what determines the emergence of a particular social system. “Socioecology frames the questions and answers in terms of how individuals’ evolved survival, mating and rearing strategies interact with the physical and social environments to produce the sort of society that we see” [Harcourt and Stewart 2007]. Socioecological theory posits that gregariousness will evolve when the net benefits of associating with conspecifics, such as improved ability to defend access to food or reduced risk of predation, outweigh the costs which include greater competition over access to resources from group members, cuckoldry, contagion, infanticide, and harassment [Alexander 1974; Clutton-Brock and Parker 1995; Janson 2000; Kappeler 1997; Krause and Ruxton 2002; Nunn and Altizer 2006; Smuts and Smuts 1993; Sterck et al. 1997; Terborgh and Janson 1986; Treves 1998; van Schaik 1983; van Schaik 1996; van Schaik and Kappeler 1997; Wrangham 1980]. The social systems exhibited by primate groups reflect the balance of these forces. Additional possible factors shaping societal patterns include cognitive constraints [Dunbar 1992] and phylogenetic inertia [Di Fiore and Rendall 1994]. It is worth emphasizing, though, that even established socioecological principles are still vulnerable to empirical refinement or even redefinitions (e.g [Thierry 2008]).

Primates show a stunning diversity of social systems [Campbell et al. 2007; Clutton-Brock and Harvey 1977; Crook and Gartlan 1966; Dunbar 1988; Eisenberg et al. 1972; Rowe 1996; Smuts et al. 1987]. Social systems include aspects of spacing and grouping characteristics and the nature and quality of social and sexual relationships among individuals [Kappeler and van Schaik 2002].

One particular type of social system, multilevel or modular societies, are structurally characterized by nuclear one-male units (OMUs) or harems which are habitually embedded within larger relatively coherent social bands. Within the order Primates, modular societies are uncommon, found in only a few species, e.g. hamadryas baboons, gelada baboons, proboscis monkeys, snub-nosed monkeys and humans. Multilevel societies are complex and among the least understood and least investigated of all the primate social systems. While the baboon system has received a fair amount of attention [Barton 2000; Barton et al. 1996; Colmenares 2004; Dunbar 1986; Dunbar and Dunbar 1975; Kummer 1968; Kummer 1990; Stammbach 1987], not much emphasis has been placed on elucidating the selective forces

leading to modular systems in colobines [Bleisch and Xie 1998; Kirkpatrick et al. 1998; Yeager 1992; Yeager and Kirkpatrick 1998]. The human social system is also organized hierarchically ([Dunbar 1989], see also [Zhou et al. 2005]), with monogamous or polygynous units amalgamating into a multifamily system [Chapais 2008].

For the examination of modular societies in colobines, I chose a dichotomous approach. In an attempt to elucidate their evolution and functional significance, I conducted a comparative cross-taxa meta-analysis, providing a phylogenetic reconstruction of modularity by means of multivariate and phylogenetically controlled comparative methods and testing predictions of socioecological hypotheses (Chapter 1). Chapter 2 deals with the predictive power of social organization/modularity on sexual dimorphism in body weight in Asian colobines.

The other part of this dissertation is a case study concentrating on Chinese black-and-white snub-nosed monkeys (*Rhinopithecus bieti*) as an exemplary model species exhibiting such a modular system. In order to elucidate the socioecological determinants or the shaping parameters of the nested system of *R. bieti*, I embarked on a 20-month field study and collected raw data on grouping patterns and sociospatial interactions (Chapter 3), forest composition, range and habitat use (Chapters 4, 5 and 6), dietary profile and strategy (Chapters 7 and 8). In Chapter 8, I also provide a preliminary assessment of the degree to which the lichenivorous-folivorous-frugivorous dietary regime of this colobine species generates the potential for feeding competition. These baseline data further contribute to a fuller comprehension of the still rudimentary knowledge of the natural history of *R. bieti* and 'fuel' comparative analyses such as the one presented in this thesis and the development of refined socioecological models. This latter point is particularly imperative since the genus *Rhinopithecus* has been omitted from virtually all comparative studies and paradigms in primatology. While data on ecology of *R. bieti* have been gathered from several sites [Cui et al. 2006c; Ding and Zhao 2004; Kirkpatrick et al. 1998; Liu et al. 2004; Ren et al. 2008; Xiang et al. 2007a; Yang 2003], our understanding of the group dynamics and underlying behavioral mechanisms is still in its infancy [Cui et al. 2008; Kirkpatrick et al. 1998; Liu et al. 2007]. The immense difficulty of following a fast-moving, wide-ranging, unhabituated group of hundreds of timid monkeys through dense mountain forests in extremely rugged terrain has contributed to the lack of data on grouping patterns and intra-and inter-sexual interactions.

A 'mini' sketch of the etho-ecology of *R. bieti* is provided here, while the subsequent chapters elaborate on some of the key concepts. *Rhinopithecus bieti* (Colobinae) is alternatively called Yunnan snub-nosed monkey or Yunnan golden monkey. This is a very large stocky sexually dimorphic semiterrestrial primate belonging to the so called 'odd-nosed colobines', a group which is now considered to represent a monophyletic clade within the Cercopithecoidea [Jablonski 2008; Sterner et al. 2006]. *Rhinopithecus bieti* has a highly restricted and fragmented distribution in the Hengduan Mountains bordering the Himalaya Range in Northwest Yunnan and Southeast Xizang (Tibet) (Long et al. 1994). Despite the species' morphological distinctiveness, endangerment (total population size ca 2000, [Long and Wu 2008]), flagship species potential and noteworthy colobine-atypical biology (see below), research efforts have been limited until the early 1990s. This is mainly a result of difficult research conditions due to the monkeys' semi-nomadic lifestyle, elusive nature and inhospitable habitat with extremely steep hillsides, impenetrable undergrowth, freezing winter climate with snow as well as damp and foggy summers with minimum visibility. Several recent studies have overcome some of the difficulties associated with studying this primate species and come up with extraordinary discoveries regarding its natural history. *Rhinopithecus bieti* lives in one of the coldest and environmentally most extreme environments of any nonhuman primate with pronounced seasonality in climate and resource availability, prompting various adaptive ecobehavioral strategies such as very narrow birth seasonality [Cui et al. 2006a; Xiang 2005], seasonal adjustments in use of altitudes [Yang 2003] or seasonal variation in daily path lengths [Ren et al., unpublished]. The habitat of the monkeys is either pure temperate coniferous forest [Zhao et al. 1988] or deciduous/evergreen broadleaf and coniferous forest [Huo 2005] at moderate to very high elevations (up to 4700 m [Long et al. 1996]. *Rhinopithecus bieti* live in very large rather cohesive super-groups which are made up of single-male core families or harems (the modular system, see above). The staple food of the monkeys are lichens [Kirkpatrick 1996], supplemented with seasonally available plant resources in more productive habitats [Ding and Zhao 2004]. Most populations have expansive home ranges [Kirkpatrick et al. 1998].

While deciphering the complex multilevel nature is the main objective of this doctorate research, a recurring side goal was to document some of the ecological and behavioral strategies that allow this species to inhabit a temperate subalpine environment that is extreme by primate standards. Among others, I illuminate to what extent use of altitudes is stratified among seasons and related to ecological variables (Chapter 3). How black-and-white snub-

nosed monkeys cope with pronounced scarcity or almost complete absence of palatable plant resources in winter is dealt with in Chapter 7.

CHAPTER 1 - Evolutionary Determinants of Modular Societies in Colobines

Introduction

Whereas in most animals living in stable and individualized social groups there are no higher levels of social organization, a few species form some kind of multilevel social systems. These modular or nested societies comprise several different kinds of distinguishable social grouping levels with varying degrees of cohesion. They have been documented in several mammal species. Thus, African elephants (*Loxodonta africana*) [Lee and Moss 2004; Moss and Poole 1983; Wittemyer et al. 2005] regularly form large aggregations of stable subunits consisting of female bonded family groups. In plains zebras (*Equus burchelli*) and khulans (*Equus hemionus*), harems regularly join to form large, spatially cohesive herds [Feh et al. 2001; Rubenstein and Hack 2004]. Other mammalian taxa with comparable multilevel social systems include sperm whales (*Physeter macrocephalus*) [Mann et al. 2000; Whitehead et al. 1991], killer whales (*Orcinus orca*) [Baird 2000] and prairie dogs (*Cynomys ludovicianus*) [Hoogland 1995].

Among primates, the foremost structural characteristics of modular systems are stable entities, usually one-male units (OMUs), which frequently or permanently associate, and thus form a higher grouping level, often termed the band ([Grüter and Zinner 2004] and references therein) (Fig. 1.1). Sociopositive and sexual behavior is largely restricted to the first tier, the OMU, while inter-unit interactions are limited (e.g. [Dunbar and Dunbar 1975; Zhang et al. 2006]. Modular societies are among the least known of all primate social systems [Barton 2000; Colmenares 2004; Stammbach 1987; Yeager and Kirkpatrick 1998].

The non-human primate species that are known to be modular in sociality are snub-nosed monkeys (*Rhinopithecus* spp.) [Kirkpatrick 1998], proboscis monkeys (*Nasalis larvatus*) [Yeager 1990], gelada baboons (*Theropithecus gelada*) [Kawai et al. 1983], hamadryas baboons (*Papio hamadryas*) [Kummer 1984] and guinea baboons (*Papio papio*) [Galat-Luong et al. 2006]. Some other taxa have been inferred to be modular, e.g. black-shanked douc langurs (*Pygathrix nigripes*) (B. Rawson & Hoang Minh Duc, pers. com.), pig-

tailed macaques (*Macaca nemestrina*) [Robertson 1986], and red uakaris (*Cacajao calvus ucayalii*) [Knogge et al. 2006].

Grüter and Zinner [2004] made a distinction between 'strict' and 'flexible' modular systems. In strict modular systems, there are typically two stable and rather closed modules, i.e. the subgroup (OMU or breeding unit) and the larger social group (band), e.g. *Papio hamadryas*. On the other hand, when OMUs congregate on an irregular basis and bands are more fluid and not as consistently assembled or behaviorally integrated as in strict modular systems, this would constitute a flexible system, e.g. *Theropithecus gelada*. However, such a dichotomous perspective does not encompass the great variability we see in different taxa, and taxa should be better placed along a continuum from more or less permanently cohesive (*Rhinopithecus bieti*) [Kirkpatrick et al. 1998] to semipermanently cohesive (*Nasalis larvatus*) [Yeager 1991a] to irregularly cohesive systems (*Trachypithecus pileatus*) [Stanford 1991a].

Modular systems contrast with classical fission-fusion societies, in which only the higher social grouping level are stable whereas subunits are flexible and unpredictable in terms of size and composition [Chapman et al. 1993; Symington 1990]. It also needs to be stressed at this point that modularity and fission-fusion are not mutually exclusive systems: a species living in a modular society may well show evidence of fission-fusion to some degree or over certain periods of time, e.g. a large modular band of *Rhinopithecus roxellana* was observed to split into two independently foraging factions, being separated by about 1 km for at least a few days ([Kirkpatrick et al. 1999]; for a similar observation in *R. bieti*, see Chapter 3 of this thesis).

Many human social and political systems are also organized hierarchically ([Dunbar 1989], see also [Zhou et al. 2005]). When my definitions are applied to humans, we are seen to combine modularity with fission-fusion. Human foragers show a trimodal structuring, with unstable foraging parties of varying composition as level 1, stable sleeping units or families at home bases as level 2, and higher levels that are rather stable and develop for purposes of ritual, politics, business, sports or warfare [Rodseth and Wrangham 2004]. The main modules within human societies are male-female bonds, which can be seen as equivalent to OMUs that are nested into a higher social alignment [Chapais 2008]. However, level 2 always contains multiple nuclear family units.

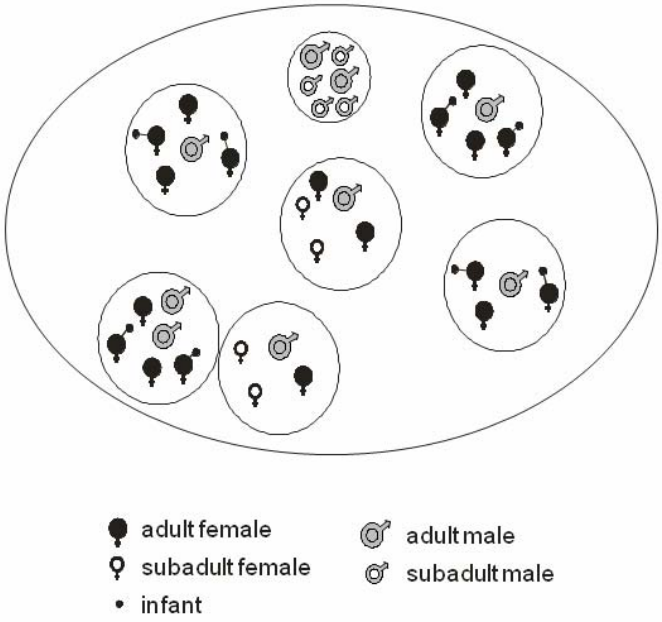


Fig. 1. 1. Structure of a modular system, exemplified by snub-nosed monkeys. The illustrated hypothetical band consists of five one-male units (OMUs) and one all-male unit (AMU).

With regard to the evolutionary origins of modular societies in primates, two putative historical pathways have been identified [Grüter and Zinner 2004]. First, the 'coalescence pathway' depicts a scenario whereby small one-male units or modules have fused to form a next higher level, i.e. a band. According to phylogenetic reconstructions, the modular system of some extant Asian colobines - most prominently represented by the snub-nosed monkeys - supposedly derives from ancestral species living in single one-male units. Groups with a single male are the norm social units in most Asian colobines [Davies and Oates 1994], so it is most parsimonious to assume that single OMUs represent the ancestral social organization of the Asian colobines ([Grüter and Zinner 2004], but see [Yeager and Kirkpatrick 1998]). Second, according to the 'divergence pathway', very large groups have fissioned into modules that are OMUs. This probably applies to certain baboon taxa, such as hamadryas baboons and geladas. There is a consensus that ancestral gelada and hamadryas baboon forms lived in savanna baboon-like multimale-multifemale groups (symplesiomorphy) that began to split into distinct OMUs for various reasons [Barton 2000; Dunbar 1986; Kummer 1990]. In

both cases, the resulting modular social system appears to be a derived feature (autapomorphy).

The presence of multiple historical pathways may reflect functional heterogeneity, and based on a preliminary review [Grüter and Zinner 2004], it is fairly unlikely that current functional bases of the modular systems in cercopithecines and colobines are the same. The baboon pathway is examined in depth in other articles [Grüter and Zinner 2004; Grüter and Zinner, in prep.], while here, we focus on the colobines.

Three forms of social organisation can be recognized in Asian colobines (Presbytini): (i) Single, often territorial OMUs with little range overlap and few inter-unit encounters (and if so, rather aggressive) (e.g. *Presbytis hosei* [Mitchell 1994], *Trachypithecus vetulus* [Rudran 1973a]). (ii) Large coherent multimale-multifemale groups (only found in *Semnopithecus* spp., e.g. [Borries 2000]); (iii) Modular societies, with OMUs having large (>40%) range overlap, at times coordinating travel and occupying adjacent sleeping trees (e.g. *Trachypithecus pileatus* [Stanford 1991a; Stanford 1991b]), or co-feeding in the same patch or adjacent patches (e.g. *Presbytis siamensis* [Bennett 1983], *Trachypithecus geei* [Mukherjee and Saha 1974]), or OMUs exhibiting complete range overlap and forming tight cohesive bands that rarely split (e.g. *Rhinopithecus bieti* [Kirkpatrick et al. 1998]). Relations among units are generally rather neutral (e.g. [Yeager 1992]). Most modular taxa share other traits that distinguish them from the non-modular ones: conspicuous sexual size dimorphism [Chapter 2 in this thesis], prominent male adornments [Grüter and Zinner 2004], large relative testes size [Grüter and Zinner 2004], large home ranges (modular colobines have significantly larger home ranges per individual (see below)), and lower population densities (see below).

In this chapter, I want to elucidate the functional determinants that have caused these higher levels of grouping in Asian colobines to emerge and be maintained. This is done via a set of predictions that are based on socio-ecological models. Classical socioecological theory considers ecological factors such as food distribution and predation risk as exerting major impacts on the spatio-temporal organization of primate females (and indirectly also of males) and their social relationships, and hence on the social system of a particular taxon [Janson and Goldsmith 1995; van Schaik 1983; Wrangham 1980]. The updated socioecological model also includes sexual conflict, in particular female coercion and infanticide by males, as a potentially critical selective factor that shapes grouping and the social systems [Chapman and

Pavelka 2005; Harcourt and Stewart 2007; Smuts and Smuts 1993; van Schaik and Janson 2000].

Phylogeny may also to some degree account for the pattern of modular societies observed in colobines. As a key example, the genus *Rhinopithecus* belongs to the odd-nosed colobines which are thought to constitute a monophyletic clade [Sterner et al. 2006]. All four *Rhinopithecus* species are typified by OMUs in bands (hence modularity), even though they live in strikingly different habitats, ranging from temperate to tropical [Bleisch and Xie 1998; Boonratana and Le 1998; Kirkpatrick 1998]. It thus seems that their social organization may partially be explained by constraining phylogenetic inertia (Di Fiore and Rendall 1994) and thus, low social plasticity, or by factors correlated with phylogeny, such as life history. The propensity to form bands from smaller units is likely an established feature of the adaptive repertoire of all *Rhinopithecus* species, expressed under a variety of present conditions. Other colobines may also have an inherent (phylogenetically maintained) capacity to create modular societies, but these are not triggered due to a lack of the necessary environmental and/or socio-sexual stimuli.

The principal aims of this article are twofold: First, I present a phylogenetic reconstruction of social systems in the Asian colobines to explore the role of phylogeny in the various social systems of Presbytini. Second, I propose several non-exclusive hypotheses (both social and ecological) that could explain why some Asian colobines developed a tendency toward modularity, i.e. increased inter-unit contact and band formation, and develop critical predictions for each of them for testing with the colobine data set. The above-mentioned evidence of low social plasticity under various environmental settings provides *prima facie* support for hypotheses that do not rely on ecological factors.

The Thermal Benefit Hypothesis

Animals can conserve heat by huddling together, because this will reduce the fraction of their surface area that is exposed to the colder surroundings [Bazin and MacArthur 1992; Krause and Ruxton 2002]. Along the lines of this widely known fact, it has been proposed that large modular bands of temperate-living colobines (specifically the Chinese snub-nosed monkeys) may have emerged for reasons of thermoregulation: living in large bands may provide more partners for thermal huddling [Bleisch and Xie 1998].

Prediction: The *prevalence of modularly constructed social systems is related to habitat temperature. The lower the mean annual temperature within the natural habitat of a given species, the higher the prevalence of modular systems.*

The Resource Dispersion Hypothesis (RDH)

The resource dispersion hypothesis posits that, if there is spatial or temporal heterogeneity in the availability of resources (which applies to most or all Asian colobine natural sites), primary residents or primary units occupying a given area will have to cover a relatively larger area to include sufficient potential resource patches to exceed some critical probability of encountering enough exploitable patches over time. Groups *per se* (or higher level social associations such as module-based bands) may form with no or minor direct costs to the original residents or original units [Bacon et al. 1991; Carr and Macdonald 1986; Johnson et al. 2002]. In other words, the resources available in the home range of the original occupant (the primary OMU) are sufficient to sustain additional OMUs. Johnson et al. [2002] point out that the RDH does not only apply to territorial species, but may potentially also explanain the social organization of species that live in large non-territorial congregations, and that the RDH requires no cooperation among units. One central precondition for the RDH is that territory size (home range size) is independent of group (band) size [Johnson et al. 2001].

Prediction 1: *Overall, home range size is not correlated with group size in Asian colobines.*

Prediction 2: *Home range size is not correlated with group size in modular Asian colobines, but correlated in non-modular ones.*

The Bachelor Threat Hypothesis

The non-ecological bachelor threat hypothesis basically posits that OMUs assemble and OMU males may form coalitions to decrease the amount of harassment, in particular the risk of takeovers and infanticide by non-reproductive bachelor groups. Such external harassment from conspecifics affects both group males and females, but in different ways: for males, danger arises because there is pressure from such non-OMU males to mate with harem females and thus challenge the reproductive monopoly of the harem male, or because the

threat of takeover increases. Females face the risk of losing their offspring in case such external males are allowed to enter the group and subsequently commit infanticide.

Rubenstein [1986] argued that bachelor threat is the most plausible scenario for the evolution of multi-level societies in plains zebras. He found that when coalitions form, female contact by bachelors was significantly lowered. Less attention has been paid to this hypothesis in primates. Wrangham [pers. com.], Mori [1979] and Dunbar and Dunbar [1975] describe hat several gelada unit leaders sometimes engaged in a collective challenge to confront and chase invading all-male groups. Treves and Chapman [1996] demonstrated that when the risk of infanticidal attack from all-male bands was high, groups of *Semnopithecus* spp. were larger and contained proportionately more adult females (but not males). Groups with more males experience a lower rate of incursion by non-resident males among red howlers (*Alouatta seniculus*) [Crockett and Janson 2000] and primates generally [Janson and van Schaik 2000].

There is ample circumstantial evidence that incursions by bachelors pose a real and significant threat to colobine unit leaders and also females. First, infanticide is an all-pervading male reproductive strategy among primates [van Schaik and Janson 2000], and also pays in seasonally breeding colobines via reduction of interbirth interval of the mother (e.g. [Borries 1997; Cui et al. 2006a]). Second, takeover and infanticide by putative bachelor males has been documented in several modularly organized colobine societies (e.g. [Agoramoorthy and Hsu 2005; Qi et al. 2008; Xiang and Grueter 2007]). Third, all-male units (AMUs) are an influential part of modular societies and habitually follow the mixed-sex bands and associate with them [Bennett and Sebastian 1988; Grüter and Zinner 2004; Hoang 2007; Kirkpatrick 1998; Stanford 1991a; Yeager 1990]. Fourth, males respond differently to other OMU males than AMU males; while encounters between reproductive units and non-reproductive units are often characterized by high levels of tension, encounters between OMUs evoke more casual responses [Boonratana 1993; Stanford 1991a]. Fifth, OMU males exhibit non-aggressive relations with extra-unit males that are known to them, i.e. encountered on a regular basis [Stanford 1991a]. In *R. bieti*, males of different OMUs are consistently in close propinquity and tend to be neutral toward each other most of the time unless a male encroaches upon another male's space (Chapter 3 in this thesis). Finally, modular species live in crowded neighborhoods, surrounded by bisexual and/or all-male units. Integrity of units may thus be compromised by the inherent threats these neighbors pose. These species are thus expected to place a premium on the maintenance of within-unit

social cohesion which is usually achieved via grooming in primates, a strategic tool that services relationships and maintains bonds [Dunbar 1991].

Prediction 1: *Presence/absence of modularity (categorical) and home range overlap (as continuous proxy variable for modularity) are positively related to the number of bachelor males in the population (cf. [Rubenstein and Hack 2004]). Assuming an even male female sex ratio at birth, the ratio F:M in bisexual units may serve as a proxy measure for bachelor threat. The higher the value, the more males are expected to be excluded from breeding units.*

Prediction 2: *The frequency of allogrooming is higher in modular societies which is based on the assumption that maintaining social bonds within units is of greater importance when bachelors and other extra-unit conspecific competitors are numerous and close by.*

Methods

The evolution of the trait modularity in the Presbytini was reconstructed in MacClade 4.07 [Maddison and Maddison 1992]. I used different rules to reconstruct character evolution: parsimony, DELTRAN (resolving states that remain ambiguous when using parsimony so as to delay changes), and ACCTRAN (forcing ambiguous reconstructions to occur closer to the root and therefore reducing the number of transitions). In the phylogram of Fig. 1.2, I consider the colobine social organization states ordered.

Information on the possible independent variables (i.e. home range size, home range overlap, sex ratio, unit size, group size, temperature, grooming frequencies) was obtained from the published literature (and unpublished theses and personal communications given) and is presented in Tab. 1.1. Raw data can be found in the Appendices to this chapter. Populations of langurs in extremely degraded and disturbed habitats (plantations, highly degraded secondary forest) were omitted from the analyses. If a population was represented by two data sets taken at different points in time, both data sets were included if the time interval between the two studies was >10 years. For the variables group size, unit size and sex ratio, I used weighted species means, i.e. means weighted by the number of groups studied, due to large differences in sample sizes. For other variables (home range size and overlap) I used means of population means. All variables (except temperature in °C and percentage of grooming) were ln-transformed prior to analysis to correct problems of unequal

variances in non-phylogenetic analyses and to meet the assumptions of independent contrasts in phylogenetic trees.

The focus lies on elucidating differences between single one-male units and aggregated one-male units. *Semnopithecus* spp. represent the only taxon of Asian colobines that exhibits a deviating social system: large multimale-multifemale groups predominate, with relatively few populations having uni-male groups. I excluded *Semnopithecus* from tests of the climate and bachelor threat hypotheses. *Semnopithecus* was, however, included in the examination of prediction 1 of the RDH because a test of this hypothesis does not require information on social organization.

Since all species with modular systems also show substantial home range overlap, I used home range overlap as a proxy measure for modularity. Such a continuous variable is better suited for testing comparative predictions than a categorical variable because it provides more fine-grained variation and is more likely to meet parametric statistical assumptions [Nunn 1999a; Nunn and Barton 2001]. Between-group encounter rate was found to be correlated with home range overlap in this sample of Asian colobines (Spearman r_s = 0.935, $p < 0.001$, $n = 11$), so there was no need of including encounter frequency as an additional variable (*pace* [van Schaik et al. 1992]).

Due to their shared ancestry, species values are often not considered to represent independent data points in comparative analyses of cross-species patterns [Abouheif 1999; Harvey and Pagel 1991; Martins and Hansen 1996]. This phylogenetic non-independence increases Type I error rates because the degrees of freedom are not properly partitioned [Pagel 1993]. Whenever sample sizes (number of species/contrasts) were sufficiently large, I thus controlled for phylogeny by means of the independent contrasts method [Felsenstein 1985], as implemented by the PDAP module [Garland et al. 1999] of the program Mesquite [Maddison and Maddison 2005].

Phylogeny used was primarily based on a molecular supertree containing estimates of divergence dates for various nodes [Bininda-Emonds et al. 2007]. Since the topology is not fully resolved for Asian colobines, additional species (for which data on the variables of interest were available) were added to the tree based on phylogenetic information obtained from other sources [Li et al. 2004; Nadler and Roos 2002; Osterholz et al. 2008; Sterner et al. 2006; Wang et al. 1997; Zhang and Ryder 1998]. If unequivocal information on divergence dates from these additional sources could not be extracted, I arbitrarily spaced nodes evenly along branches (cf. [Plavcan 2004]). In a few cases taxonomic information alone was used to

construct a topology, e.g. the four *Semnopithecus* species considered here, which were formerly considered to be single species, are treated as pairs of sister species here. This was done under the assumption that groups at a given taxonomic level are of comparable age.

Since the independent contrast method is relatively robust to inaccuracies in the available phylogenetic information (branching sequence, branch lengths) and since mostly terminal branches were unresolved, such ambiguities have been found to hardly affect the outcome of the analysis [Martins and Garland 1991]. When repeating the contrast analysis under a 'punctuated evolution' model, i.e. setting all branch lengths equal to 1, the results did not differ in the level of significance from the ones presented here. Absolute contrasts were also standardized by dividing them by the square root of the sum of the branch lengths. This was done because the further back on the roots of the tree, towards the most primitive character states, the contrasts are more and more removed from the observed values and are estimated through an averaging process. Thus, the estimated primitive characters states were given less weight than the topmost states ([Garland et al. 1999], cf. [Barrickman et al. 2008]). Contrasts were statistically analyzed with least squares regression, and following standard practice, contrasts slopes were forced through the origin [Garland et al. 1992].

Comparative analyses were also performed using species data, i.e. without controlling for phylogeny. Both nonphylogenetic and phylogenetic results are reported. I used a General Linear Model (GLM) to simultaneously assess the effect of several predictor variables on the dependent variable and ANCOVA to test for a relationship between a grouping variable and a dependent variable while including a third variable as a covariate. Analyses were run in JMP 7 and SPSS 16.0. All probabilities reported are for two-tailed tests. Statistics were considered significant at $p < 0.05$.

Results

Some Characteristics of Modular and Non-modular Colobines

Modular colobines were found to have significantly larger home ranges (in ha) per individual (means: 4.3 vs. 9.7; $U_{13, 9} = 29.00$, $p = 0.049$), and lower population densities (mean no. of individuals per km^2: 64.9 vs. 18.5; $U_{7, 11} = 12.00$, $p = 0.016$) than non-modular ones. A compilation of various socioecological data of Asian colobines is given in Tab. 1.1.

Tab. 1.1. List of various socioecological traits of Asian colobines used for the analyses in this chapter.

Species	Unit size	Band size	AF/ AM[1]	Soc Org	OM/ MM[2]	HR size[3]	%HR overlap	Temp (°C)	% Groom
Presbytis comata	6.7	NA	1.9	non-mod	OM	26	9	16.0	UNK
Presbyis siamensis	15.1	NA	3.9	mod	MM	22	41	27.7	0
Presbytis thomasi	8.9	NA	3.6	non-mod	OM	38	41	25.8	UNK
Presbytis potenziani	3.8	NA	1.2	non-mod	OM	23	34	28.0	0.3
Presbytis rubicunda	6.4	NA	2.7	non-mod	OM	65	12	27.4	0
Presbytis hosei	7.5	NA	2.5	non-mod	OM	40	10	27.1	UNK
Trachypithecus auratus	14.2	NA	5.4	non-mod	OM	10	23	26.3	UNK
Trachypithecus obscurus	17	NA	2.4	non-mod	MM	33	3	27.7	UNK
Trachypithecus geei	10.7	NA	4.9	mod	OM	228	UNK	UNK	2.3
Trachypithecus vetulus	8.9	NA	3.3	non-mod	OM	7	UNK	20.5	UNK
Trachypithecus johnii	7	NA	3.4	non-mod	MM	63	10	14.9	0.1
Trachypithecus phayrei	14.3	NA	3.5	non-mod	MM	47	UNK	UNK	7.2
Trachypithecus leucocephalus	10.3	NA	4.5	non-mod	OM	37	16	22.1	11
Trachypithecus pileatus	8.6	NA	3.0	mod	OM	22	84	24.9	1.9
Trachypithecus francoisi	9.5	NA	1.6	non-mod	MM	44	UNK	22.0	2
Semnopithecus achates	28.2	NA	6.2	large mm-mf	MM	68	0	24.0	4
Semnopithecus entellus	21.2	NA	5.9	large mm-mf	MM	233	50	24.4	6
Semnopithecus schistaceus	23.7	NA	3.2	large mm-mf	MM	553	UNK	16.6	7
Semnopithecus priam	29.4	NA	3.2	large mm-mf	MM	90	UNK	27.9	UNK
Simias concolor	5.2	NA	1.9	non-mod	OM	15	8	28.5	UNK
Rhinopithecus bieti	8.3	210	4.1	mod	OM	1940	100	5.5	6.7
Rhinopithecus roxellana	13	215	4.5	mod	OM	2570	100	7.5	11.6
Rhinopithecus brelichi	6.2	400	2.2	mod	OM	3500	100	11.0	UNK
Rhinopithecus avunculus	12.9	80	4.8	mod	OM	1300	100	22.1	5.6
Pygathrix nemaeus	23.7	UNK	2.8	UNK	MM	258	UNK	25.0	UNK
Pygathrix nigripes	11.3	UNK	2.1	mod	MM	48	10	26.5	2.4
Nasalis larvatus	13.4	30	6.4	mod	OM	359	94	26.8	2.2

[1] AF = adult female, AM = adult male.

[2] OM = one-male, MM = multi-male.

[3] HR = home range.

The data were extracted from the following sources:

Presbytis comata: [Ruhiyat 1983]; *Presbytis siamensis*: [Bennett 1983; Bennett 1986; Johns 1983]; *Presbytis thomasi*: [Assink and van Dijk 1990; Sterck and van Hooff 2000; van Schaik et al. 1992]; *Presbytis potenziani*: [Fuentes 1994; Fuentes 1996; Sangchantr 2004; Watanabe 1981]; *Presbytis rubicunda*: [Bennett and Davies 1994; Davies 1984; Davies 1987; Salafsky 1988; Supriatna et al. 1986; van Schaik et al. 1992; Waterman et al. 1988]; *Presbytis hosei*: [Mitchell 1994; Nijman 2004]; *Trachypithecus auratus*: [Kool 1989; Vogt 2003]; *Trachypithecus obscurus*: [Curtin 1980]; *Trachypithecus geei*: [Biswas 2002; Chetry et al. 2002; Medhi et al. 2004; Srivastava 2006; Srivastava et al. 2001]; *Trachypithecus vetulus*:

[Rudran 1973a; Rudran 1973b]; *Trachypithecus johnii*: [Bennett and Davies 1994; Hohmann 1989; Horwich 1972; Joseph and Ramachandran 2003; Oates et al. 1980; Poirier 1968; Poirier 1969a; Poirier 1969b; Poirier 1970; Tanaka 1965]; *Trachypithecus phayrei*: [Borries et al. 2004; Bose and Bhattacharjee 2002; Gupta 2002; Gupta and Kumar 1994; Pages et al. 2005]; *Trachypithecus leucocephalus*: [Huang and Li 2005; Li and Rogers 2004a; Li and Rogers 2004b; Li and Rogers 2005]; *Trachypithecus pileatus*: [Biswas et al. 2004; Green 1981; Solanki et al. 2007; Stanford 1991a; Stanford 1991b]; *Trachypithecus françoisi*: [Huang et al. 2006; Zhou et al. 2006; Zhou et al. 2007]; *Semnopithecus achates*: [Borries et al. 1994; Chhangani and Mohnot 2006; Hrdy 1977; Jay 1965; Moore 1985; Newton 1988; Rahaman 1973; Reena and Ram 1992; Ross and Srivastava 1994; Srivastava and Dunbar 1996; Starin 1978; Sugiyama 1964; Vogel 1973; Vogel 1977]; *Semnopithecus entellus*: [Bennett and Davies 1994; Hrdy 1977; Jay 1965; Moore 1985; Newton 1987; Newton 1992; Oppenheimer 1977; Srivastava and Dunbar 1996; Sugiyama 1967]; *Semnopithecus schistaceus*: [Bishop 1975 ; Bishop 1979; Boggess 1980; Borries and Koenig 2000; Curtin 1982; Sugiyama 1976]; *Semnopithecus priam*: [Moore 1985; Ross 1993; Srivastava and Dunbar 1996]; *Simias concolor*: [Tenaza and Fuentes 1995; Tilson 1977; Watanabe 1981]; *Rhinopithecus bieti*: [Cui et al. 2008; this thesis; Huo 2005; Kirkpatrick 1996; Kirkpatrick et al. 1998; Liu et al. 2007; Xiang 2005a; Yang 2000; Ren B unpublished]; *Rhinopithecus roxellana*: [Hu et al. 1980; Kirkpatrick and Gu 1999; Li et al. 2000; Li et al. 1995; Lu and Li 2006; Ren et al. 1998; Ren et al. 2000; Su et al. 1998; Tan et al. 2007; Zhang et al. 2006]; *Rhinopithecus brelichi*: [Bleisch et al. 1993; Bleisch and Xie 1998]; *Rhinopithecus avunculus*: [Boonratana and Le 1998; Dong and Boonratana 2006; Kirkpatrick 1998; Le et al. 2006; Le and Boonratana 2006]; *Pygathrix nemaeus*: [Lippold 1977; Lippold 1998; Pham 1993]; *Pygathrix nigripes*: [Eames and Robson 1993; Hoang 2007; Lippold 1998; Phan et al. 2005; Rawson 2006; B Rawson pers. com.]; *Nasalis larvatus*: [Agoramoorthy and Hsu 2005; Bennett and Sebastian 1988; Boonratana 1993; Boonratana 2000; Boonratana 2002; Murai et al. 2007; Yeager 1989a; Yeager 1989b; Yeager 1990].

The most frequent social system is given.
Whenever data on home range size and overlap were given as ranges rather than averages, I took the midpoint.
If no annual mean temperature was given, I used the mean of annual minima and maxima or estimated it from graphs.
Values for the variables 'group size', 'unit size' and 'sex ratio' represent species means weighted by the number of groups studied. Values for 'home range size' and 'overlap' represent means of population means.
The social organization of *Pygathrix nemaeus* is treated as unknown since available reports are mixed.
For *Nasalis*, band size was calculated based on the average size of one-male units and average number of units with which OMU was associated (usually 2).
For additional information on data extraction criteria, see Methods.

Historical Origins of Modularity

Reconstruction of the social organization of the Presbytini (with Colobini as an outgroup) confirms that a non-modular system was ancestral and modularity is a derived feature (Fig. 1.2.). DELTRAN, ACCTRAN and parsimony all yielded the same pattern. Modularity evolved three or four times independently in the Presbytini: twice in the odd-nosed colobines (but if we assume a monophyletic relationship for the odd-nosed colobines [Sterner et al. 2006], then only once), once in *Presbytis* (*Presbytis siamensis*) and once in *Trachypithecus* (*T. geei* and *T. pileatus*). Modularity was likely lost secondarily in *Simias*, which have a tiny geographical distribution on the Mentawai Islands, possibly because its

groups are very small due to the absence of feline predators or because recent anthropogenic infiltration and hunting has reduced population numbers of this species to a level where modularity cannot be expressed anymore (cf. [Watanabe 1981]). Strict modularity is phylogenetically confined to the odd-nosed colobines.

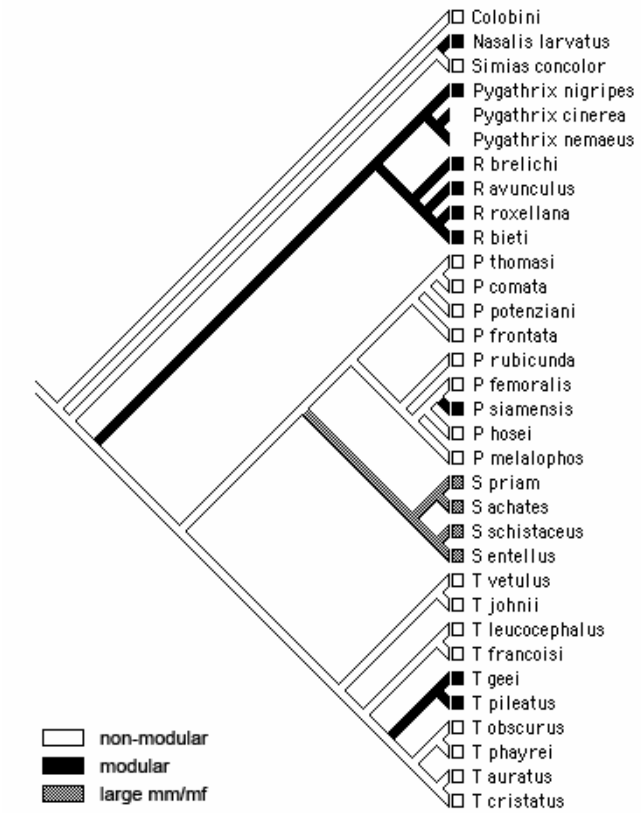


Fig. 1.2. Colobine phylogeny, indicating the distribution of the three character states as defined in the text. Phylogeny is based on [Bininda-Emonds et al. 2007], with terminal branches having been modified after [Li et al. 2004; Nadler and Roos 2002; Osterholz et al. 2008; Sterner et al. 2006; Wang et al. 1997; Zhang and Ryder 1998], where necessary. Note that the phylogenetic relation of the *Nasalis*-*Simias* branch with regard to the other colobines differs between the composite estimate of Purvis [1995] and the supertree of Bininda-Emonds et al. [2007].

Climate Hypothesis

By comparing average annual habitat temperatures of modular vs. non-modular colobine species, I found no statistical difference (t test, $t = 1.54$, $p = 0.141$, $df = 18$) (Fig.

1.3). More importantly, modular societies were common in tropical climates, where animals would rarely if ever need to form big huddles to minimize heat loss.

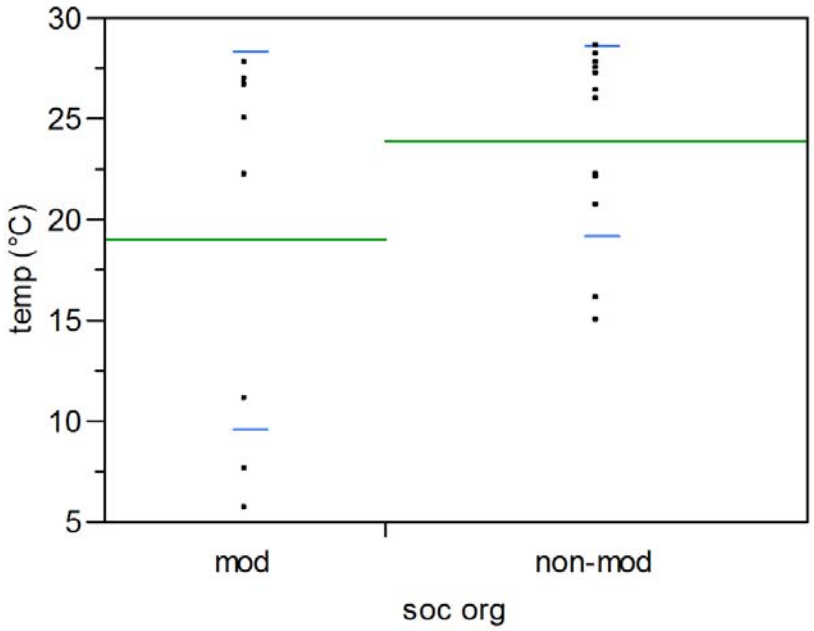


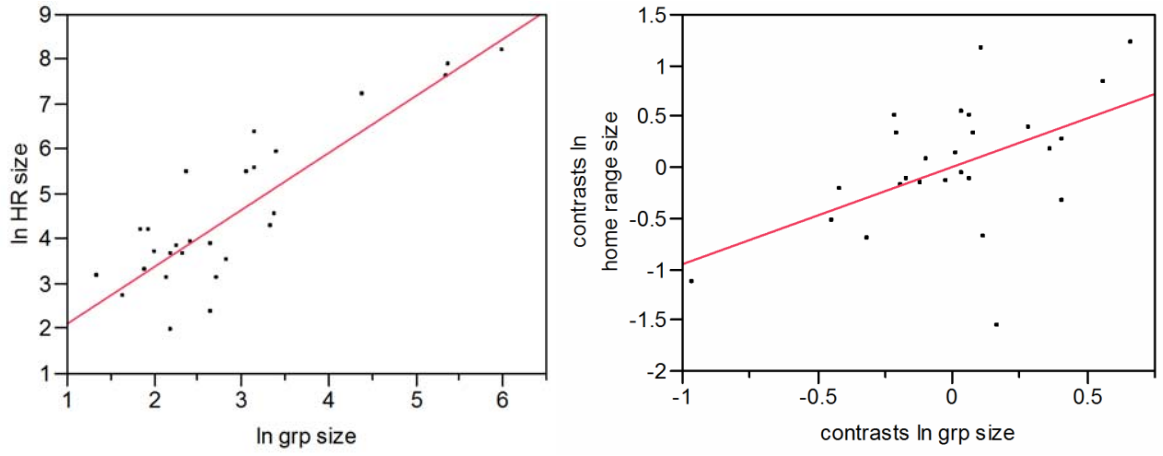
Fig. 1.3. Mean annual habitat temperature (°C) of modular vs. non-modular Asian colobine species. Means and standard deviations.

Resource Dispersion Hypothesis

Prediction 1: When entering the non-phylogenetic data (species data points) in a single regression analysis (with ln group size as the independent variable and ln home range size as the dependent one), the following equation was obtained:

ln home range size = 0.85 + 1.27 x ln group size ($F_{1,25} = 73.97$, $p < 0.0001$, $R^2 = 0.747$) (Fig. 1.4a)

Using the independent contrasts, group size remained a significant predictor of home range size ($F = 9.1785$, $p = 0.006$) (Fig. 1.4b).



(a) (b)

Fig. 1.4. (a) Ln home range size regressed against ln group size in Asian colobines. (b) Plot of independent contrasts in ln home range size and ln group size for Asian colobines.

Using ANCOVA, I tested for a relationship between habitat productivity (temperate vs. tropical; the grouping variable) and home range size (dependent variable) while including group size as a covariate (Fig. 1.5). Since the interaction group size*productivity did not have a significant effect on home range size ($p = 0.235$), I calculated the ANCOVA model without the interaction effect. Group size then had a significant positive effect on home range size ($F = 22.50$, $p < 0.0001$, $df = 1$), whereas habitat did not have a significant effect on home range size ($F = 1.59$, $p = 0.219$, $df = 1$).

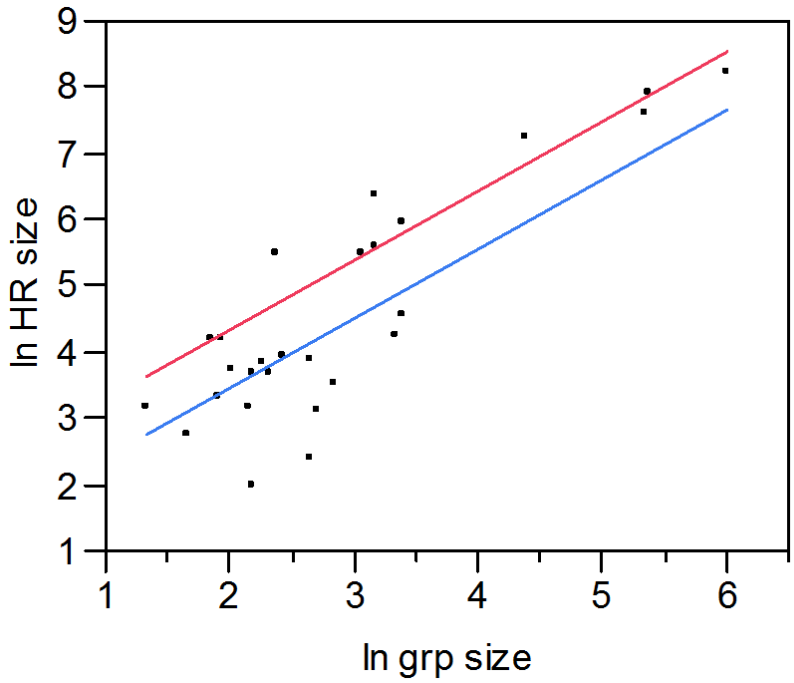


Fig. 1.5. Ln home range size plotted against ln group size in Asian colobines. The regression lines were drawn through the data from tropical-living (lower line) and temperate-living species (upper line), respectively.

Prediction 2: When analyzing the data separately for modular and non-modular colobines (no contrast analysis is provided due to the low number of contrasts), there was a strong positive correlation between group size and home range size for the modular ones ($F = 37.4377$, $p = 0.0005$), but no correlation for the non-modular ones ($F = 0.1434$; $p = 0.7128$).

Bachelor Threat Hypothesis

Prediction 1: There was a nearly significant difference in sex ratio of bisexual groups (proxy measure for bachelor threat) between the categorical variables modular vs. non-modular (t test, $t = -1.965$, $p = 0.063$, $df = 20$) (Fig. 1.6).

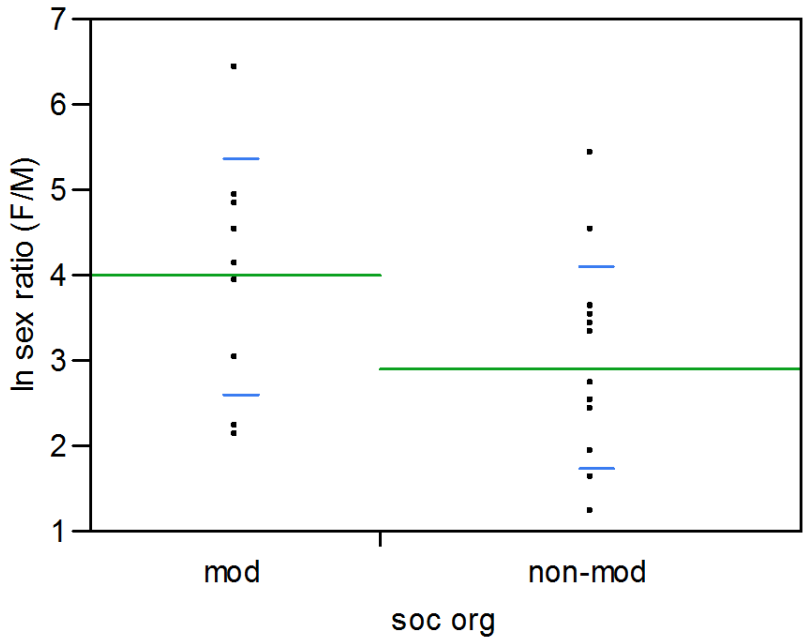
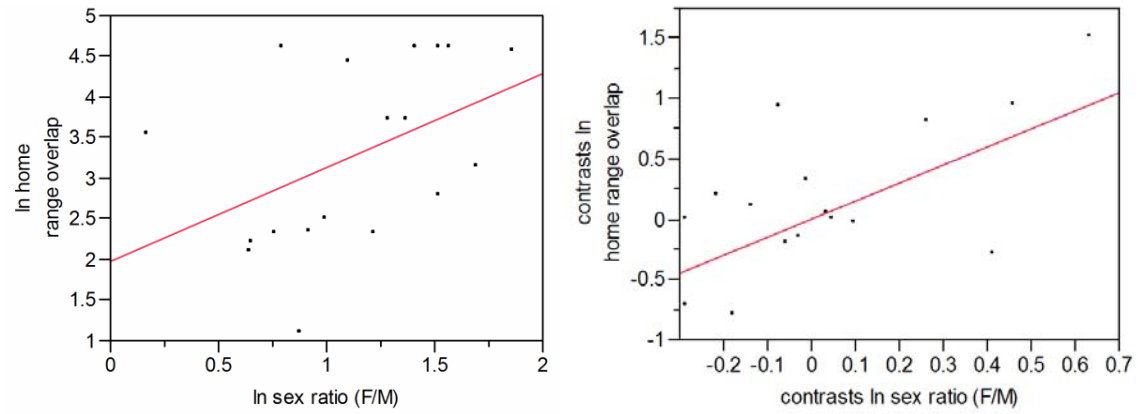


Fig. 1.6. Sex ratio (F/M) of bisexual groups compared between modular and non-modular colobines. Means and standard deviations.

When using home range overlap as a continuous proxy measure for modularity, sex ratio of bisexual groups showed a nearly significant positive correlation with home range overlap ($F_{1,16} = 4.14$, $p = 0.059$, $R^2 = 0.206$). The regression equation would be:

ln home range overlap = 1.97 + 1.16 x ln sex ratio (Fig. 1.7a)

After removal of phylogenetic dependence, this relationship became highly significant (F ratio = 11.52, p = 0.004) (Fig. 1.7b).



(a) (b)

Fig. 1.7. Association beween home range overlap and sex ratio (F/M) in Asian colobines. (a) Species data, (b) independent contrasts.

When I included unit size as a potentially confounding variable in a multiple regression analysis, the above relation still held rather well, i.e. the model was almost significant ($F = 3.06$, $p = 0.0632$, $R^2 = 0.396$). Sex ratio remained the only significant predictor of the dependent variable ln home range overlap ($p = 0.0224$), while ln unit size and the interaction between unit size and sex ratio had no significant effect ($p = 0.3764$, 0.1822, respectively). Using the independent contrasts data, the whole model remained significant ($F = 6.58$, $p = 0.005$), with contrasts in ln sex ratio being significantly related to contrasts in ln home range overlap ($p = 0.022$) and contrasts in ln unit size ($p = 0.108$), and the interaction between the two ($p = 0.130$) not having a significant effect.

Prediction 2: Modular and non-modular colobines did not differ with regard to the percentage of grooming in the activity budget ($U_{6,5} = 8$, $p = 0.201$; phylogenetically uncorrected data).

Discussion

The Thermal Benefit Hypothesis

The climate hypothesis was rejected based on the above meta-analysis of temperature data. There are additional arguments against this hypothesis. First, it is doubtful whether the

thermal benefit gained from aggregating with more than one module is substantial, and I assume that within-module huddling provides sufficient heat. Vickery and Millar [1984] showed that the extra gain that each individual receives from another joining the huddle decreases with increasing group size. Second, since OMUs are discrete social entities, no huddling involving more than one unit is expected to occur. In both *Rhinopithecus roxellana* and *R. bieti*, members of each OMU huddle and sleep together separately from other units in the larger group to which they belong [Chen et al. 1989; Qi et al. 2004; Chapter 3 in this thesis]. Spatial distances among individuals from different social units are considerably longer than those among individuals from the same social unit [Qi et al. 2004]. Third, Kirkpatrick et al. [1998] found no connection at all between ambient temperature and frequency of huddling in wild *R. bieti*. Fourth, rhinopiths may have lived at lower (warmer) elevations [Li B et al. 2002a] where there was no need for assembling as a means of thermoregulation, before being forced higher up the mountains by human pressure. Fifth, all rhinopith populations (i.e. the ones living at high latitude/altitude and the ones living at lower latitude/altitude) appear to show essentially the same modular social grouping pattern [Kirkpatrick 1998]. Sixth, modular colobines are typically arboreal or semi-arboreal, and arboreality naturally prevents large huddling groups from forming because a single tree rarely supports more than one OMU. And finally, *R. bieti* lives in seasonally freezing climate, but the bands seem to be equally cohesive year round [Kirkpatrick et al. 1998]. In other words, larger groups do not form distinctively during the cold season as expected by the climate hypothesis.

The Resource Dispersion Hypothesis

There was a strong positive correlation between group size and home range size for the modular colobines. If the RDH had explanatory potential for band formation, then we would expect the opposite, i.e. no correlation between group size and home range size in modular colobines (Prediction 2).

The first prediction of the resource dispersion hypothesis is that home range size is independent of group size in all Asian colobines. According to my analyses, this basic prediction is not met. I found a positive association between group and home range size for Asian colobines (*pace* [Yeager and Kirkpatrick 1998]). This indicates the existence of resource competition [Janson and van Schaik 1988; Nunn and Barton 2000]. This is due to

the fact that an increase in the size of a group causes a larger biomass of consumers per unit area. In order to sustain per capita energy intakes, the quantity of available resources must be enlarged. Resource competition is probably a consequence of ephemeral (seasonal) foods and not (abundant) staple foods. Despite the apparent pervasiveness of scramble competition, large modular societies do exist. I thus have reasons to believe that some other benefit of sociality overwhelms the disadvantage of increased scramble competition and home range expansion [Macdonald and Carr 1989]. A potential counterbalancing selective factor might be bachelor threat, a form of social pressure.

The Bachelor Threat Hypothesis

My results of the correlations between the number of bachelors and prevalence of modularity indicate that bachelor threat may well be of significant importance in colobines living in nested societies. No support, though, was found for the prediction that modular colobines show higher grooming frequencies. Nevertheless, all strongly modular rhinopiths spend a considerable amount of their time allogrooming (*R. roxellana*: 11.6%, *R. bieti*: 6.7%, *R. avunculus*: 5.6%; references in the Appendix). Reliable data on grooming frequencies are generally scarce for Asian colobines and additional data are needed for a more conclusive test. I would also expect males to be more socially integrated into the unit, i.e. being in closer proximity to other unit members to ensure efficient surveillance and protection from rivals from outside the family unit**.** The paucity of data does not allow this prediction to be tested at the moment.

The bachelor threat model has been applied successfully to equids [Rubenstein and Hack 2004]. The explanatory power of the bachelor threat hypothesis for modular colobines would be enhanced if unit holders could actually be seen collectively defending the group against incursions from bachelor males. Incidents of collective male defense in modular colobines have not been reported in the literature so far, or been observed (C. Stanford, C. Tan, I. Matsuda, T. Murai, C. Yeager, pers. com.). They may thus be nonexistent or they are not readily or easily identified because of their subtlety or the extremely difficult observation conditions that characterize most study sites (poor habituation, dense foliage etc.) or simply because modular colobines have been the focus of only very few studies (a notable exception being *Nasalis*). I do, however, have one observation from our study on *R. bieti* that can be interpreted as collective (but not necessarily collaborative) aggression of males against

intruders: an OMU leader was seen attacking a non-unit individual, and then another leader of a neighboring OMU also started displaying towards the same target individual (Grueter, pers. obs.). Moreover, a case where several units jointly attacked a male (but not an AMU male) was witnessed in a semi-provisioned group of *R. roxellana* (*ibid*.).

Even though male cooperation does not appear to be common in modular colobine societies, this does not necessarily invalidate the bachelor threat hypothesis. First, it is possible that males of different units do not need to show deliberate coordination against bachelors. Sterck and van Hooff [2000] mention that langur males "seem neither to check the actions of other males nor to coordinate their behavior with other males actively, [but] they may well act in parallel because similar behavior is triggered by the same stimulus (e.g. [Curtin 1980] for banded langurs)". Second, even if intentional cooperation is not exhibited by males in bands, a benefit for males may accrue simply for numerical reasons: the probability of being targeted and ousted by bachelors declines as band size increases. This is similar to the dilution effect, a supposedly adaptive response to predation [Caro 2005; Pulliam and Caraco 1984].

In a mountain gorillas group containing two silverbacks, the older one was more likely to ignore opposing groups during intergroup encounters and let the other take the risk of fighting [Robbins and Sawyer 2007]. This has been interpreted as a collective action problem [Nunn 2000]. The absence of collaborative action against intruding males may be reconciled with such a collective action problem in snub-nosed monkeys as well. In geladas, it was often one unit leader at a time who initiated an attack on the bachelors and only rarely several unit leaders in tandem [Mori 1979; Dunbar 1984, pp. 177-178].

The principle of OMU leaders gathering together for safety reason is similar to the acceptance of 'follower' males, as found in some OMU-based equid and primate societies. In some equids, male followers at times also help dominant stallions to protect females against harassment by outside males and to hold off outside males from matings with band females [Asa 1999; Berger 1986; Feh 1999; Miller 1981; Stevens 1990]. In mountain gorillas, follower males lower the risk of takeovers and subsequent infanticide [Robbins 2001; Sicotte 2001; Watts 2000]. In hamadryas baboons, there is some evidence that males belonging to a clan cooperate to prevent non-clan males from kidnapping females (Sigg et al. 1982). In chimpanzees, males cooperatively defend estrous females from mating with other males. Males engage in this strategy when the number of group males reaches a certain threshold and single males are no longer able to monopolize the females on their own [Watts 1998a].

In gelada baboons, Dunbar [1984] has suggested that by allowing an extra male to join the harem as a follower, the current leader may reduce the chances of his unit being the target of a takeover attempt by a bachelor male and may thus prolong his tenure as a breeding male. Dunbar [1984, p. 177] explains that "the benefits that unit holders derive from accepting a follower have nothing to do with the latter's playing any active role in supporting the unit leader during takeover attempts by rival males. It seems to work, however, because harems with followers reduce the *effective* size of the units (i.e., the number of unit females actually bonded with the harem male), thus increasing the females' loyalty to the leader and reducing the probability of being evicted by other males." The same reasoning may be appropriate for a modular colobine system.

Another factor that may also have an effect on the formation of bands is kinship among units. A network of kin among those units in a band may facilitate OMUs keeping closer together. In proboscis monkeys, one-male units form differentiated relationships in which they tolerate some groups but not others [Yeager 1989b, 1991]. Stanford [1991a] observed the same in capped langurs and hypothesized that genetic relatedness may be a factor affecting male tolerance. Investigating such kinship factors among units in a modular colobine society would reward us with a better understanding of how these complex societies operate.

Other Hypotheses

Other hypotheses are not addressed here in detail because they are less easy to characterize in quantitative terms and they are unlikely to be relevant. To complete the picture, though, they are briefly discussed below.

The *harvest efficiency*, *resource depletion* or *Cody/Altmann hypothesis* ([Cody 1971; Altmann 1974], see also [Rodman 1988]) suggests that for primates, feeding in a group rather than independently, maximizes individual feeding efficiency by minimizing returns to exhausted patches. This hypothesis has occasionally been invoked as a potential explanation of group living in primates in general [Isbell 2004]. Also for polyspecific associations, it has been argued that groups of one species join groups of another to avoid areas where the first species has recently foraged, thereby increasing foraging efficiency [Cords 1987; Enstam and Isbell 2007]. Kirkpatrick et al. [1998] argue that the depletion problem may be of particular significance in species such as *R. bieti* which inhabit habitats where food resources are plenty

and homogenous but regeneration time is low. An area that has been picked clean of lichens - the staple food of *R. bieti* - requires at least two decades to regenerate. By forming large bands where all individuals and units visit the same feeding area, individual snub-nosed monkeys or units minimize the chances of foraging in an area where lichens have been eaten up recently. While this scenario may apply to some populations living in habitats with slowly regenerating foods, I doubt that it is an all-encompassing explanation for modularity in all colobines.

A problem that is inherent in this hypothesis is that subordinate units (facing competition with higher-ranking units) may fare better when separating and foraging independently and not following dominant units. Independent foraging may be associated with occasional costs due to ignorant visits of an already depleted patch (cf. [Harcourt and Stewart 2007]), but especially when they visit dispersed patches of fruiting trees or leafing trees, foraging in a group of several hundred will undoubtedly lead to substantial competition for access to these trees which can only accommodate a part of the group. Some very large units (probably dominant units) seemed to defend such trees for a while (Chapter 8 in this thesis). So harvest efficiency is not assumed to be a primary selective factor or an evolutionary stable strategy.

The Cody/Altmann hypothesis seems to work better for primate species with no home range overlap, because then the risk of unknown, unscheduled visits by others is non-existent. While home range overlap between bands is minimal or absent in snub-nosed monkeys (e.g. [Kirkpatrick et al. 1998]), the very large groups of associated subunits would only increase the chance of individuals or subunits crossing each other's feeding paths and thereby offset the proposed benefit of preventing visits to depleted patches (cf. [Harcourt and Stewart 2007]). Through theoretical modelling it has also been borne out that group foragers obtain food at lower rate than solitary foragers, i.e. reduced avoidance of patches already visited by others failed to overcome the increased time cost of searching for new food patches [Beauchamp 2005].

The *localized resource hypothesis* (LRH) (cf. Dunbar 1986) posits that highly localized essential or ephemeral resources such as water sites, shelters or food attract several OMUs or force OMUs to congregate at such places. Such resources may be only seasonally available or consistently rare within the habitat. If localized resources were indeed of explanatory value, we would expect the units only to assemble temporally when these resources are available or in spatially restricted places, i.e. fission-fusion should be common.

Given that the modular construction is a persistent feature in at least the strictly modular colobines, this may at best be an explanation for the loose neighborhoods found in some colobine species. For instance, the number of inter-group encounters in *Presbytis siamensis* increased when the animals fed more in large and rare food trees (i.e. widely-spaced and seasonal and large food trees) [Bennett 1983]. Overall, though, exploitation of localized resources does not uniformly explain band formation.

Localized resources may, though, be an ecological basis that has brought independent social units to come closer together and favoured nested grouping patterns. Localized resources are likely of particular importance in strongly seasonal environment such as in high-elevation forests of the temperate zone with fluctuating availability of (food) resources and heterogeneous vegetation distribution (e.g. Chapter 4 in this thesis). These biota are inhabited by some of the modular colobines, most notably three species of rhinopiths (*R. bieti*, *R. roxellana*, *R. brelichi*). Such an environment may provoke social units to forage in that part of the habitat where resources are obtainable. This in turn may lead to overlap of home ranges which I regard to be a necessary basis for bringing initially separate OMUs into closer proximity. However, this is just a prerequisite and not a satisfactory explanation for the emergence or maintenance of modularity.

If we extend the localized resource hypothesis to the hominin 'home base' or 'central place foraging' model [Isaac 1982], then it can be seen as an ecological precondition for the emergence of modularity in humans. Frequent use of highly localized resources may have led to the adoption of home-base sites in hominids (cf. [Moore 1996; Layton and Barton 2004]). Inferring that refugia became limited in the increasingly open and patchy savanna habitat that our ancestors dwelled in, this may have promoted return use of certain areas (e.g. riverine strips, valleys, rocks) for sleeping, drinking, feeding or safety reasons (e.g. [Marlowe 2006]).

I would like to stress that localized resources certainly seem to attract passive aggregations (that are not necessarily social groups *per se*) which can be made up of OMUs. Gelada herds on mountain grasslands are not reported to be social groups in the strict sense, but rather temporary congregations of OMUs at sites where grazing conditions are favorable. Herds are largest during the dry season when the availability of food is spatially restricted [Dunbar 1993]. Another example are transitory troops of hamadryas baboons clustering at cliffs [Kummer 1968], which - similar to gelada herds - are not genuine individualized social groups. Human families/OMUs also aggregate in order to exploit extremely localized

resources, e.g. water in arid habitats: Australian Western Desert Aboriginal groups and Kalahari Bushmen cluster around water holes in times of drought [Long 1971; Lee 1972].

Yeager [1992] proposed that *between-band resource competition* may be a factor for the modular social system in *Nasalis larvatus*, i.e. that units may associate with other units to avoid displacement by other bands at feeding or sleeping sites. In the genus *Rhinopithecus*, interband competition does not seem to be strong [Kirkpatrick et al. 1998]: for example, Bleisch and Xie [1998] found that bands of *R. brelichi* at Fanjingshan did not compete when they encountered each other but that, contrariwise, bands fused together. Bands of *R. roxellana* in the Qinling region had little range overlap, though bands encountered each other at some feeding sites, apparently without aggression [Chen et al. 1989]. However, it was recently advanced by Li Y et al. [2002] that the resource competition model of Wrangham [1980] may be apt to explain the habitat use of *R. roxellana* bands at Shennongjia: it seemed to be the case that larger bands occupied higher quality habitat and large home ranges due to their ability to compete successfully with smaller groups for preferred feeding sites (large groups were found in high quality mature forest whereas small groups were confined to low quality young forest).

In line with the *predation avoidance hypothesis*, protection from predation has been seen as a major aggregative force in primates (van Schaik 1983). Several lines of evidence, though, signify that predation is a relatively insignificant threat to Asian colobines living in modular groups: first, in a comparative assessment, it has been shown that predation is less important for Asian langurs compared to howlers and African colobus monkeys [van Schaik and Hörstermann 1994]. Second, the large body size of most modular colobines makes them partially or fully immune to predation. The odd-nosed colobines are among the heaviest extant monkeys and do not seem to have many natural enemies capable of preying upon them (e.g. [Grüter and Zinner 2004; Kirkpatrick et al. 1998]); notable exceptions are birds of prey and clouded leopards which, however, seem to be a menace to youngsters only [Zhang et al. 1999; Cui 2003b; Matsuda et al. 2008a]. Third, the semi-terrestrial habitus of *R. bieti* and *R. roxellana* (Kirkpatrick and Long 1994; Ren et al. 2001) may indicate a reduced predator pressure. In *R. bieti*, for instance, all age/sex classes (including infants) occasionally rest on the ground (Grueter, pers. obs.).

Band formation in *Nasalis larvatus* has been hypothesized to be a response to increased predation risk, i.e. temporary associations may allow groups to coordinate river crossings, thereby reducing individual risk of predation by crocodilians (dilution affect)

[Yeager 1991b, 1992], see also [Boonratana 1992]). However, the fact that bands of OMUs occur at a site with predators and without predators [Yeager 1995] and that units sometimes remain in association when travelling inland [Bennett and Sebastian 1988] makes this rationalization somewhat less convincing.

Many tropical langurs live in small isolated OMUs despite the presence of arboreal feline predators such as clouded leopards in these habitats, and this justifies the dismissal of predation as a significant influence on band formation in Asian colobines. Predation may well work to explain presence of OMUs rather than solitaries or pairs, but not very large bands, since the group size benefit from predation quickly saturates. Overall, safety from predators may at best be a subsidiary and not the main benefit of associating into bands (cf. [Hinde 1982]). Nevertheless, it is worth reminding that present predation risk and rate in any population does not necessarily reflect the former predation regime that selected the current anti-predation strategy and respective social organization [Cheney and Wrangham 1987].

According to the *reproductive facilitation hypothesis*, enhanced access to potential mates is considered a benefit ensued from aggregating in bands [Grüter and Zinner 2004; Yeager and Kool 2000]. Onuma [2002] proposes that getting together at river banks in proboscis monkeys offers opportunities for males to display and for females to meet and assess males of other OMUs (*mate assessment hypothesis*). These latter two hypotheses are highly speculative and compelling empirical substantiation is lacking.

In sum, ecological conditions did not seem to determine the formation of bands in Asian colobines. Nevertheless, the fact that modular bands are habitually large in size does require an abundant and non-localized resource base that permits the formation of bands in the first place. Staple foods of many modular colobines appear to be fairly abundant (e.g. lichens in *Rhinopithecus bieti* [Chapter 7 in this thesis; Kirkpatrick et al. 1998] or leaves in *Nasalis larvatus* [Boonratana 1993; Matsuda et al. 2008b], so no forbidding foraging costs are imposed by assembling. On the other hand, my results have shown that feeding competition effects are present and mostly result from seasonal non-staple foods. By eliminating ecological benefits, I considered the threat of intruding bachelor males as a plausible scenario, which was found to be consistent with most known facts, but needs to be strengthened by further *in situ* observations.

Appendix

Appendix 1: Home range variables for Asian colobines

Species	Locality	Home range size (ha)	Home range overlap (%)	Encounter frequency (#/hr)	References
Presbytis comata	Kamojang	38	9	0.0352	[Ruhiyat 1983]
Presbytis comata	Patenggang	14			[Ruhiyat 1983]
Presbyis siamensis	Kuala Lompat (1970/71)	21	19	0.002	[Curtin 1980]
Presbyis siamensis	Kuala Lompat (1981)	30	79	0.077	[Bennett 1983; Bennett 1986]
Presbyis siamensis	Sungai Tekam [1]	14	24		[Johns 1983]
Presbytis thomasi	Ketambe (1989) [2]	37.7	40.5	0.0205	[Assink and van Dijk 1990; Sterck and van Hooff 2000; van Schaik et al. 1992]
Presbytis potenziani	Betumonga	33	40 [3]		[Fuentes 1994; Fuentes 1996]
Presbytis potenziani	Muntei	22.5	28	0.011	[Sangchantr 2004]
Presbytis potenziani	Grukna/Sarabua	13.25			[Watanabe 1981]
Presbytis rubicunda	Gunung Palung (1987) [4]	37.8	12	0.0342	[Salafsky 1988]
Presbyis rubicunda	Tanjung Puting (1975)	70.8	14 [5]		[Supriatna et al. 1986]
Presbytis rubicunda	Sepilok	85	10	0.0045	[Bennett and Davies 1994; Davies 1984; Davies 1987; van Schaik et al. 1992; Waterman et al. 1988]
Presbytis hosei	Lipad	40	10.2		[Mitchell 1994]
Trachypithecus auratus	Pangandaran	7.25 [6]	23		[Kool 1989]
Trachypithecus auratus	West Bali NP	13.7	23		[Vogt 2003]
Trachypithecus obscurus	Kuala Lompat	33	3	0.0028	[Curtin 1980]
Trachypithecus geei	-	25 [7]			[Biswas 2002]
Trachypithecus geei	Assam [8]	430			[Srivastava 2006]
Trachypithecus vetulus	Horton Plains	6.8			[Rudran 1973a; Rudran 1973b]
Trachypithecus johnii	Kakachi	24	10		[Bennett and Davies; Oates et al. 1980]
Trachypithecus johnii	Periyar	7.1			[Horwich 1972]
Trachypithecus johnii	Ootacamund	157			[Kirkpatrick 2007; Poirier 1968; Poirier 1969a; Poirier 1970]
Trachypithecus phayrei	Sepahijala	20			[Gupta 2002]
Trachypithecus phayrei	Phu Khieo	74			[Pages et al. 2005]
Trachypithecus leucocephalus	Fusui [9]	37.3	16.2		[Li and Rogers 2004a; Li and Rogers 2005]
Trachypithecus pileatus	Madhupur (1986-88)	22	84	0.08	[Stanford 1991a; Stanford 1991b]
Trachypithecus francoisi	Fusui	19			[Zhou et al. 2006]
Trachypithecus francoisi	Nonggang	69		0.0014	[Zhou et al. 2006]
Semnopithecus achates	Dharwar (open)	149			[Sugiyama 1964]
Semnopithecus achates	Dharwar (closed)	19			[Sugiyama 1964; Sugiyama 1976]
Semnopithecus achates	Gir [10]	40	0		[Rahaman 1973; Starin 1978]

Semnopithecus achates	Sariska	60			[Vogel 1973; Vogel 1977]
Semnopithecus achates	Kumbhalgarh	74			[Chhangani and Mohnot 2006]
Semnopithecus entellus	Orcha	390			[Bennett and Davies 1994; Hrdy 1977; Jay 1965; Moore 1985; Oppenheimer 1977]
Semnopithecus entellus	Kanha (meadow)	75	50		[Newton 1987; Newton 1992]
Semnopithecus schistaceus	Junbesi	1250 [11]			[Curtin 1982]
Semnopithecus schistaceus	Melemchi	218			[Bishop 1975; Bishop 1979]
Semnopithecus schistaceus	Simla/Hatto	190			[Sugiyama 1976]
Semnopithecus priam	Wilpattu	100 [12]			[Muckenhirn 1972]
Semnopithecus priam	Polonnaruwa	80 [12]			[Moore 1985]
Simias concolor	N. & S. Pagai	13.5			[Kirkpatrick et al. 1998; Tenaza and Fuentes 1995]
Simias concolor	Grukna	3.5	8 [14]		[Watanabe 1981]
Simias concolor	Sirimuri	27.5			[Tilson 1977]
Rhinopithecus bieti	Xiaochangdu	2125	100	1 [15]	[Xiang 2005]
Rhinopithecus bieti	Mt. Longma	956	100	1 [15]	[Huo 2005]
Rhinopithecus bieti	Mt. Fuhe	1070	100	1 [15]	[Liu et al. 2004]
Rhinopithecus bieti	Wuyapiya	2525	100	1 [15]	[Kirkpatrick et al. 1998]
Rhinopithecus bieti	Jinsichang	1730	100	1 [15]	Ren et al. in prep
Rhinopithecus bieti	Samage	3231	100	1 [15]	This study
Rhinopithecus roxellana	Shennongjia	2600	100	1 [15]	[Ren et al. 1998; Su et al. 1998]
Rhinopithecus roxellana	Zhouzhi (East Ridge Troop)	1830	100	1 [15]	[Tan et al. 2007]
Rhinopithecus roxellana	Baihe	3600	100	1 [15]	[Kirkpatrick and Gu 1999]
Rhinopithecus roxellana	Zhouzhi (West Ridge Troop)	2250	100	1 [15]	[Li et al. 2000]
Rhinopithecus avunculus	Ta Ke	1000	100 [16]		[Boonratana and Le 1994]
Rhinopithecus avunculus	Khau Ca	1600			[Le et al. 2006]
Rhinopithecus brelichi	Fanjingshan	3500	100	1	[Bleisch et al. 1993; Bleisch and Xie 1998]
Pygathrix nigripes	Nui Chua NP/Phuoc Binh NP	47.5	10		[Hoang 2007]
Pygathrix nemaeus	-	258			[Pham 1993]
Nasalis larvatus	Sukau/Abai	267	100 [16]	0.69 [17]	[Boonratana 1993; Boonratana 2000]
Nasalis larvatus	Menanggul River	138			[Matsuda et al. 2008b]
Nasalis larvatus	Samunsam	900	87	0.7 [17]	[Bennett and Sebastian 1988]
Nasalis larvatus	Tanjung Puting	130	96	0.66 [18]	[Yeager 1989a; Yeager 1989b; Yeager 1990]

1 Situation before logging.

2 Estimates based on data from the intensively sudied western half of study area. Home range size and overlap based on the 2 long-term study groups only.

3 ~40.

4 Home range size and overlap not based on quadrats but on minimum convex polygon method.

5 Range overlap estimated using density and mean home range size.

6 Home range size is based on no of 0.25 ha quadrats used. Data for groups in reserve only (excluding data on provisioned groups).

7 An annual value for home range size was obtained by avergaing seasonal values (given).

8 Data from undisturbed habitat only.

9 Only data from 3 groups with >86 positional records were used (another intensively studied group was omitted from the analysis because it lived in extremely degraded habitat (lowest quality habitat I)); for each of the 3 groups a mean overlap with all neighboring groups was calculated.

10 Home range datum from [Srivastava and Dunbar 1996].

11 Home range size computed with a 0.4 x 0.4 ha grid.

12 Home range datum taken from [Srivastava and Dunbar 1996].

13 Up to 19.

14 Overlap estimated from Fig.2.

15 I arbitrarily chose '1' as the encounter rate because units are in more or less constant proximity to one another.

16 ~100.

17 Between-group encounter rate is based on % of nights 2 groups slept in proximity (within 100 m).

18 Between-group encounter rate based on mean percent of sightings in which groups were in association.

Appendix 2: Mean annual temperature at Asian colobine sites

Species	Site	Temperature (°C)	Reference
Presbytis comata	Kamojang	16	[Ruhiyat 1983]
Presbytis comata	Patenggang	16	[Ruhiyat 1983]
Presbyis siamensis	Kuala Lompat (1981)	27.7	[Bennett 1983]
Presbyis femoralis	Perawang (1984)	26.5	[Megantara 1989]
Presbytis thomasi	Bohorok	26.7	[Gurmaya 1986]
Presbytis thomasi	Ketambe (1989)	24.9	[Assink and van Dijk 1990]
Presbytis potenziani	Betumonga	29.4	[Fuentes 1994]
Presbytis potenziani	Muntei	26.5	[Sangchantr 2004]
Presbyis rubicunda	Tanjung Puting (1975)	27.6	[Supriatna et al. 1986]
Presbytis rubicunda	Sepilok	27.2	[Davies 1984]
Presbytis hosei	Lipad	27.1	[Mitchell 1994]
Trachypithecus auratus	Pangandaran	26.3	[Kool 1989]
Trachypithecus obscurus	Kuala Lompat	27.7	[Curtin 1980]
Trachypithecus vetulus	Polonnaruwa	26	[Rudran 1973a; Rudran 1973b]
Trachypithecus vetulus	Horton Plains	15	[Rudran 1973a; Rudran 1973b]
Trachypithecus johnii	Ootacamund	14.9	[Poirier 1970]
Trachypithecus leucocephalus	Fusui	22.1	[Huang and Li 2005]
Trachypithecus pileatus	Madhupur (1986-88)	24.9	[Stanford 1991a; Stanford 1991b]
Trachypithecus francoisi	Nonggang	22	[Zhou et al. 2007]
Semnopithecus achates	Dharwar (open)	24	[Srivastava and Dunbar 1996]
Semnopithecus achates	Kaukori	25.9	[Jay 1965]
Semnopithecus achates	Jodhpur	27	[Hrdy 1977]
Semnopithecus achates	Jaipur	25.1	[Reena and Ram 1992]
Semnopithecus achates	Dharwar (closed)	24	[Srivastava and Dunbar 1996]
Semnopithecus achates	Sariska	25	[Srivastava and Dunbar 1996]
Semnopithecus achates	Kumbhalgarh	22.8	[Srivastava and Dunbar 1996]
Semnopithecus achates	Abu forest	17.9	[Srivastava and Dunbar 1996]
Semnopithecus achates	Gir	26.8	[Srivastava and Dunbar 1996]
Semnopithecus achates	Ranthambore	21.7	[Srivastava and Dunbar 1996]
Semnopithecus entellus	Orcha	21.4	[Srivastava and Dunbar 1996]
Semnopithecus entellus	Raipur	26.9	[Sugiyama 1964]
Semnopithecus entellus	Singur	27	[Oppenheimer 1977]
Semnopithecus entellus	Kanha (meadow)	23.3	[Srivastava and Dunbar 1996]
Semnopithecus entellus	Deotalao	23.3	[Srivastava and Dunbar 1996]
Semnopithecus schistaceus	Junbesi	9.5	[Srivastava and Dunbar 1996]
Semnopithecus schistaceus	Melemchi	17.7	[Srivastava and Dunbar 1996]
Semnopithecus schistaceus	Ramnagar	25.4	[Srivastava and Dunbar 1996]
Semnopithecus schistaceus	Simla	13.6	[Srivastava and Dunbar 1996]
Semnopithecus schistaceus	Hatto	13.6	[Srivastava and Dunbar 1996]
Semnopithecus priam	Wilpattu	27.7	[Srivastava and Dunbar 1996]

Semnopithecus priam	Polonnaruwa	28	[Srivastava and Dunbar 1996]
Semnopithecus hector	Bhimtal	13.9	[Srivastava and Dunbar 1996]
Semnopithecus hector	Rajaji	20.1	[Srivastava and Dunbar 1996]
Simias concolor	Grukna	28.5	[Watanabe 1981]
Rhinopithecus bieti	Wuyapiya	0.9	[Kirkpatrick 1996]
Rhinopithecus bieti	Xiaochnagdu	4.7	[Xiang 2005]
Rhinopithecus bieti	Longma	8.8	[Huo 2005]
Rhinopithecus bieti	Xiangguqing	7.5	[Ding and Zhao 2004]
Rhinopithecus roxellana	Wolong	6.3	[Hu et al. 1980]
Rhinopithecus roxellana	Shennongjia	5	[Ren et al. 1998; Ren et al. 2000]
Rhinopithecus roxellana	Baihe	7.5	[Kirkpatrick and Gu 1999]
Rhinopithecus roxellana	Zhouzhi	10.7	[Qi et al. 2008]
Rhinopithecus avunculus	Ta Ke	22.1	[Kirkpatrick 1998]
Rhinopithecus brelichi	Fanjingshan	11 [1]	[Bleisch et al. 1993; Bleisch and Xie 1998]
Pygathrix nemaeus	Son Tra	25	[Lippold 1977]
Pygathrix nigripes	Phuoc Binh NP	26.5	[Hoang 2007]
Nasalis larvatus	Sukau	27	[Boonratana 1993]
Nasalis larvatus	Samunsam	26.5	[Bennett and Sebastian 1988]

[1] Climate data estimated from Fig. 2 in [Bleisch and Xie 1998].

Appendix 3: Group size and composition in Asian langurs

Species	Locality	No. groups [15]	Unit size	Band size	#AM[16] /group	#AF[16] /group	References
Presbytis comata	Kamojang	4	7.8		1	3	[Ruhiyat 1983]
Presbytis comata	Patenggang	5	5.8		1.2	1.4	[Ruhiyat 1983]
Presbyis siamensis	Kuala Lompat (1981)	3	15		1	7.7	[Bennett 1983; Bennett 1986]
Presbyis siamensis	Kuala Lompat (1970/71)	5	15.9		2.3	5.8	[Curtin 1980]
Presbyis siamensis	Sungai Tekam	3	14		1	5.7	[Johns 1983]
Presbytis thomasi	Ketambe (1989)	7	8.9		1	3.6	[Assink and van Dijk; Sterck and van Hooff 2000; van Schaik et al. 1992]
Presbytis potenziani	Betumonga	10	3.3		1	1	[Fuentes 1994; Fuentes 1996]
Presbytis potenziani	Muntei	12	4.6		1.3	1.8	[Sangchantr 2004]
Presbytis potenziani	Grukna	10	3.4		1	1	[Watanabe 1981]
Presbyis rubicunda	Tanjung Puting (1975)	9	6.1		1	2.6	[Supriatna et al. 1986]
Presbyis rubicunda	Gunung Palung (1987)	1	9		1	4	[Salafsky 1988]
Presbytis rubicunda	Sepilok	1	7		1	2	[Bennett and Davies 1994; Davies 1984; Davies 1987; van Schaik et al. 1992; Waterman et al. 1988]
Presbytis hosei	Lipad [1]	2	7.5		1	2.5	[Mitchell 1994]
Trachypithecus auratus	Pangandaran	9	14.4		1.2	6.6	[Kool 1989]
Trachypithecus auratus	West Bali NP [2]	2	13.5		1	6	[Vogt 2003]
Trachypithecus obscurus	Kuala Lompat	2	17		2.5	6	[Curtin 1980]
Trachypithecus geei	Jamduar	7	12.7		1.1	5.1	[Mukherjee and Saha 1974]
Trachypithecus geei	Raimona	2	15.5		1	6.5	[Mukherjee and Saha 1974]
Trachypithecus geei	Manas RF [3]	12	10.9				[Srivastava et al. 2001]
Trachypithecus geei	Manas NP [3]	7	7				[Srivastava et al. 2001]
Trachypithecus vetulus	Horton Plains	20	8.9		1	3.3	[Rudran 1973a; Rudran 1973b]
Trachypithecus johnii	Ootacamund [4]	8	9.5		1.5	3.4	[Poirier 1969b; Poirier 1970]
Trachypithecus johnii	Anaimalai	3	8		1.3	2.7	[Hohmann 1989]
Trachypithecus johnii	Mundanthurai	9	11.1		1.3	4.4	[Hohmann 1989]
Trachypithecus johnii	Periyar	4	15.4		1	8	[Tanaka 1965]
Trachypithecus johnii	Silent Valley NP	85	5.9				[Joseph and Ramachandran 2003]
Trachypithecus phayrei	Phu Khieo	1	9		1	4	[Pages et al. 2005]
Trachypithecus phayrei	Gumti Sanctuary	5	15.4		1.4	4.6	[Gupta and Kumar 1994]
Trachypithecus leucocephalus	Fusui [5]	9	10.3		1.1	5	[Li and Rogers 2004b; Li and Rogers 2005]
Trachypithecus pileatus	Madhupur (1986-88)	9	8.2		1	3.6	[Stanford 1991a; Stanford 1991b]
Trachypithecus pileatus	Madhupur (1976)	13	9		1.1	3	[Green 1981]
Trachypithecus pileatus	Pakhui	1	8		1	5	[Solanki et al. 2007]
Trachypithecus	Nonggang	1	12		4	5	[Zhou et al. 2007]

francoisi							
Trachypithecus francoisi	Fusui	1	7		1	3	[Huang et al. 2006]
Semnopithecus achates	Dharwar (open)	10	15.3		1	8.5	[Sugiyama 1964]
Semnopithecus achates	Dharwar (closed)	26	15.5		1.5	7.8	[Sugiyama 1964]
Semnopithecus achates	Sariska	12	37.7		1 [6]	17.6	[Ross and Srivastava 1994; Srivastava and Dunbar 1996]
Semnopithecus achates	Sariska [7]	4	64		13	33.5	[Vogel 1973; Vogel 1977]
Semnopithecus achates	Abu Forest	11	35		1.7	10.5	[Hrdy 1977; Moore 1985; Newton 1988]
Semnopithecus achates	Gir [8]	10	30.4		2.4	13.6	[Rahaman 1973; Starin 1978]
Semnopithecus achates	Ranthambore	7	43		2.7	22.9	[Moore 1985]
Semnopithecus entellus	Orcha	3	19		3.7	6	[Bennett and Davies 1994; Hrdy 1977; Jay 1965; Moore 1985; Oppenheimer 1977]
Semnopithecus entellus	Kanha (meadow)	14	21.7		1.1	9.1	[Newton 1987; Newton 1992]
Semnopithecus entellus	Deotalao [9]	4	21		1	10.5	[Newton 1987]
Semnopithecus schistaceus	Junbesi	6	11		2	3.4	[Bishop 1975] [Boggess 1980]
Semnopithecus schistaceus	Melemchi	1	32		4	8	[Bishop 1975] [Bishop 1979]
Semnopithecus schistaceus	Ramnagar	18	18.3		2.5	6.6	[Borries and Koenig 2000]
Semnopithecus schistaceus	Simla	7	39		2.9	11.9	[Sugiyama 1976]
Semnopithecus schistaceus	Hatto	3	43		2.7	19.7	[Sugiyama 1976]
Semnopithecus priam	Wilpattu	7	25.1		3	11.1	[Muckenhirn 1972]
Semnopithecus priam	Mundanthurai	4	37		5.2	14.3	[Ross 1993]
Simias concolor	Pagai	20	4.05		1.05	1.9	[Tenaza and Fuentes 1995]
Simias concolor	Grukna	9	7.9		1	2.1	[Watanabe 1981]
Simias concolor	Siberut	2	9		1	2.5	[Hadi et al. 2008]
Simias concolor	Sirimuri	5	3.5		1	1	[Tilson 1977]
Rhinopithecus bieti	Tacheng (Xiangguqing) [10]	19 (1)	11.3	366	1	4.7	[Ding et al. 2004; Liu et al. 2007]
Rhinopithecus bieti	Deqin	67 (2)	7.5	146	1	4	[Cui et al. 2008]
Rhinopithecus bieti	Jinsichang	(1)		180			[Ren et al. 2008]
Rhinopithecus bieti	Fuhe	(1)		80			[Liu et al. 2004]
Rhinopithecus bieti	Longma	(1)		80			[Huo 2005]
Rhinopithecus bieti	Xiaochangdu	(1)		210			[Xiang 2005]
Rhinopithecus bieti	Samage	(1)		410			This study
Rhinopithecus roxellana	Shennongjia [11]	(1)	18	340	1.06	7	[Ren et al. 2000]
Rhinopithecus roxellana	Baihe	3 (1)	12	400	1.3	4.7	[Kirkpatrick and Gu 1999]
Rhinopithecus roxellana	Zhouzhi (West Ridge Troop)	8 (1)	9	82	1	3.3	[Zhang et al. 2006]
Rhinopithecus roxellana	Baishuijiang	(1)		80			[Li et al. 1995]
Rhinopithecus roxellana	Zhouzhi (East Ridge Troop)	(1)		112			[Tan et al. 2007]
Rhinopithecus roxellana	Wolong	(1)		275			[Hu et al. 1980]
Rhinopithecus brelichi	Fanjingshan	15 (1)	6.2	400	1	2.2	[Bleisch et al. 1993; Bleisch and Xie 1998]
Rhinopithecus avunculus	Na Hang	5 (1)	15.2	80	1	4.8	[Kirkpatrick 1998]
Rhinopithecus	Khau Ca	(1)	10.5	81	1	UNK	[Le and Boonratana 2006]

avunculus							
Pygathrix nemaeus	Son Tra	3	9.3		1.3	3.7	[Lippold 1977]
Pygathrix nemaeus	Phu Mat	3	30.3				[Lippold 1998]
Pygathrix nemaeus	Bach Ma	3	13.3				[Lippold 1998]
Pygathrix nemaeus	Kon Kai Kinh	1	51				[Lippold 1998]
Pygathrix nemaeus	Kon Cha Rang	1	51				[Lippold 1998]
Pygathrix nigripes	Kon Cha Rang	1	36				[Lippold 1998]
Pygathrix nigripes	Nui Cha	36	13.1		1.55	3.25	[Hoang 2007]
Pygathrix nigripes	Phuoc Binh	17	10.1		1.4	3.1	[Hoang 2007]
Pygathrix nigripes	Cat Tien NP	17	6.9				[Phan et al. 2005]
Pygathrix nigripes	Nui Pantar	-	12.5				[Eames and Robson 1993]
Pygathrix nigripes	Deo Nui San	1	20				[Eames and Robson 1993]
Nasalis larvatus	Sukau	6	17	34 [12]	1	7.3	[Boonratana 1993; Boonratana 2000; Boonratana 2002]
Nasalis larvatus	Samunsam	6	9	18 [12]	1	3.7	[Bennett and Sebastian 1988]
Nasalis larvatus	Tanjung Puting	10	12.6	38 [13]	1	5	[Yeager 1989b; Yeager 1990]
Nasalis larvatus	Labuk Bay	1	36	NA	1	14	[Agoramoorthy and Hsu 2005]
Nasalis larvatus	Menanggul River	2	18 [14]	NA	1	14.5	[Murai et al. 2007]

1 Group composition data based on Dec 1991.

2 Group size at beginning of study.

3 Undisturbed.

4 From 8 bisexual troops on whom accurate counts of all age and sex categories were obtained.

5 Group living in extremely degraded (lowest quality habitat I) not included.

6 No. males per group was not given by [Ross and Srivastava 1994] and [Srivastava and Dunbar 1996], but all 12 groups were apparently unimale (Ross in [Moore 1985]).

7 Values taken from [Newton 1988].

8 Group composition data taken from [Newton 1988].

9 Values taken from [Treves and Chapman 1996]; includes subadult females.

10 Gully crossing data.

11 Tables difficult to read and understand in that publication; data based on group progressions; since no data on sample size are given, I use normal means instead of weighed means.

12 Band size was calculated based on the average size of OMUs and average number of units with which OMU was associated, i.e. 2.

13 Band size was calculated based on the average size of OMUs and average number of units with which OMU was associated, i.e. 3.

14 Group size after female immigration.

15 No. bands in parentheses.

16 AM = adult male, AF = adult female.

CHAPTER 2 - Sexual Size Dimorphism in the Colobinae Revisited

Introduction

Body weight dimorphism in mammals has been thought to be a consequence of sexual selection resulting from male-male competition for access to mates (e.g. [Alexander et al. 1979; Clutton-Brock and Harvey 1978]. Mitani et al. [1996a] confirmed this for anthropoids living in multi-male groups. Plavcan and van Schaik [1997] classified the intensity of male contest competition over mates into four competition categories, based on two levels for frequency and intensity of potential escalated contest, and concluded that body weight dimorphism was strongly associated with these competition levels. They recognized that several colobine primates (e.g. *Nasalis larvatus*) show substantial levels of body weight dimorphism, whereas other harem-living species in *Presbytis* were virtually monomorphic (see also [Plavcan 2001]. Plavcan and van Schaik were not able to offer any compelling explanation for the pattern in colobine weight dimorphism. They added: "Understanding the evolution of weight dimorphism in this group should provide substantial insight into mechanisms governing the evolution of dimorphism in all primates." The highly dimorphic genus *Rhinopithecus* (Fig. 2.1) was not included in the study of Plavcan and van Schaik [1997].

In this chapter, I re-evaluate the connection between competition and body weight dimorphism (SD) for colobines. Specifically, I examine the effect of 'modularity.' I recognize two forms of social organisation (two inter-unit association degrees) in colobines: (i) Single OMUs with little range overlap and few inter-unit encounters (and if so, usually aggressive) (e.g. *Presbytis hosei* [Mitchell 1994]), henceforth called 'non-modulars'. (ii) Modular societies, with OMUs having large (>40%) range overlap, at times coordinating travel and occupying adjacent sleeping trees (e.g. *Trachypithecus pileatus* [Stanford 1991a; Stanford 1991b], or co-feeding in the same patch or adjacent patches (e.g. *Presbytis siamensis* [Bennett 1983]; *Trachypithecus geei* [Mukherjee and Saha 1974]), thus forming a second level called the band. The degree of band cohesion varies somewhat among colobines, with *R. bieti* units on the one end exhibiting complete home range overlap and forming tight

cohesive bands that rarely split, and others showing 'loose neighbourhoods' (e.g. *Trachypithecus pileatus* [Stanford 1991a]). Relations among units are generally rather neutral (e.g. [Yeager 1992]). Another type of social system, large coherent multimale-mulifemale groups, are found only in *Semnopithecus* spp. (e.g. [Borries 2000]).

The effect of modularity is to bring colobine one-male units (OMUs) in more or less permanent proximity. This increase in association should increase the frequency of opportunities for escalated male contest over mating access to females or female membership of these OMUs. Moreover, these OMUs are shadowed more or less continuously by all-male units, which threaten to take over the OMUs or engage in extra-group matings with the unit females. For these two reasons, I predict that male-male competition is both more frequent and more intense in modular societies than in other types of colobine social systems. In the following, I explore the potential effects of modularity as well as other predictor variables on the magnitude of SD in Asian colobines.

(a) (b)

(c)

Fig. 2.1. Three species of *Rhinopithecus*, all of which show high levels of sexual dimorophism in body mass. (a) *Rhinopithecus roxellana*, (b) *R. brelichi*, and (c) *R. bieti*. All photos © C. C. Grueter.

Methods

Data on SD (expressed as the ratio of mean male and female body mass) as well as potential predictor variables (home range overlap, social organization, unit size and composition, substrate and breeding seasonality) were obtained from the literature (Tab. 2.1). If a population of langurs was represented by two data sets taken at different points in time, both data sets were included, but only if the time interval between the two studies was >10 years. All continuous variables were natural log transformed prior to analysis. The multimale-multifemale system, the modal grouping pattern of *Semnopithecus* spp., is included as a distinct category in an analysis investigating the differences in SD among the 3 social systems of Asian colobines. The remaining analyses of the effect of various predictor variables on SD are restricted to modular and non-modular species.

The dichotomous variables modular vs. non-modular were used for one analysis. Since all species with modular systems also show substantial home range overlap and home range overlap can thus be regarded as a proxy measure for modularity, I also conducted an analysis using this continuous variable. Such a continuous variable is assumed to better suited

for testing comparative predictions than a categorical variable because it provides more fine-grained variation and is more likely to meet parametric statistical assumptions [Nunn 1999a; Nunn and Barton 2001].

Breeding seasonality is included as a predictor variable because, on theoretical grounds, we would expect more intense competition among males in highly seasonal breeders. This reasoning is based on the assumption that competition intensity correlates with priority of access which itself is often affected by breeding seasonality (Mitani et al. 1996b).

Due to their shared ancestry, species values are often not considered to represent independent data points in comparative analyses of cross-species patterns [Harvey and Pagel 1991; Martins and Hansen 1996]. I thus controlled for phylogeny by means of the independent contrasts method [Felsenstein 1985], as implemented by the PDAP module [Garland et al. 1999] of the program Mesquite [Maddison and Maddison 2005]. It calculated evolutionary changes ('contrasts') over branches of the phylogeny such that each contrast is fully independent of other contrasts and is thus suitable for standard statistical analysis.

Phylogeny used was primarily based on a molecular supertree containing estimates of divergence dates for various nodes [Bininda-Emonds et al. 2007]. Since the topology is not fully resolved for Asian colobines, additional species (for which data on the variables of interest were available) were added to the tree based on phylogenetic information obtained from other sources [Li et al. 2004; Osterholz et al. 2008; Sterner et al. 2006; Wang et al. 1997; Zhang and Ryder 1998].

I performed the contrast analysis under a 'punctuated evolution' model, i.e. setting all branch lengths equal to 1. To test the adequacy of this model, I plotted the absolute values of contrasts for each variable vs. the standard deviation (i.e. the square root of the sum of its branch lengths) to validate that the algorithm accurately scales branch lengths (cf. [Garland et al. 1992]). The slopes were not significantly different from zero for all variables, and independent contrast assumptions were thus not violated when setting branch lengths to 1. Then, absolute contrasts were standardized by dividing them by the square root of the sum of the branch lengths. Thus, the contrasts between estimated primitive characters states were given less weight than the topmost contrasts ([Garland et al. 1999], cf. also [Barrickman et al. 2008]). Contrasts were statistically analyzed with least squares regression, and following standard practice, contrasts slopes were forced through the origin [Garland et al. 1992].

Comparative analyses were also performed using species data, i.e. without controlling for phylogeny. Both nonphylogenetic and phylogenetic results are presented. I used multiple

regressions to simultaneously assess the effect of several predictor variables on the dependent variable. Analyses were run in JMP 7.0.2 (SAS Inc.) and SPSS 16.0. All probabilities reported are for two-tailed tests. Statistics were considered significant at $p < 0.05$.

Tab. 2.1. Data on social organization (modular vs. non-modular), body weight dimorphism (SD), unit size and composition (one-male vs. multi-male), arboreality vs. terrestriality, home range overlap and breeding seasonality for all Asian colobines for which the relevant data are available[4].

Species	Social Org	SD	Unit size	Unit composition[1]	Substrate[2]	Home range overlap (%)	Breeding seasonality[3]
Presbytis comata	Non-mod	1.01	6.7	OM	A	9	No
Presbyis siamensis	Mod	1.02	15.1	MM	A	41	
Presbytis thomasi	Non-mod	1.01	8.9	OM	A	41	No
Presbytis potenziani	Non-mod	1.02	3.8	OM	A	34	
Presbytis rubicunda	Non-mod	1.05	6.4	OM	A	12	
Presbytis hosei	Non-mod	1.11	7.5	OM	A	10	
Trachypithecus obscurus	Non-mod	1.19	17	MM	A	3	No
Trachypithecus geei	Mod	1.15	10.7	OM	A		
Trachypithecus vetulus	Non-mod	1.21	8.9	OM	A/T		No
Trachypithecus johnii	Non-mod	1.20	7	MM	A	10	Yes
Trachypithecus phayrei	Non-mod	1.08	14.3	MM	A		
Trachypithecus leucocephalus	Non-mod	1.12	10.3	OM	A/T	16	
Trachypithecus pileatus	Mod	1.21	8.6	OM	A	84	No
Trachypithecus francoisi	Non-mod	1.05	9.5	MM	A/T		
Semnopithecus entellus	Multimale-multifemale	1.31	21.2	MM	A/T		No
Semnopithecus schistaceus	Multimale-multifemale	1.30	23.7	MM	A/T		Yes
Semnopithecus priam	Multimale-multifemale	1.65	29.4	MM	A/T		
Simias concolor	Non-mod	1.23	5.2	OM	A	8	
Rhinopithecus bieti	Mod	1.68	8.3	OM	A/T	100	Yes
Rhinopithecus roxellana	Mod	1.74	13	OM	A/T	100	Yes
Rhinopithecus brelichi	Mod	1.86	6.2	OM	A	100	
Rhinopithecus avunculus	Mod	1.75	12.9	OM	A	100	
Pygathrix nigripes	Mod	1.03	11.3	MM	A	10	
Nasalis larvatus	Mod	2.09	13.4	OM	A	94	No

[1] OM = one-male, MM = multi-male.

[2] A = arboreal, A/T = arboreal and terrestrial.

[3] Breeding seasonality is defined as greater than 67% of births in a single 3-month period (cf. [Nunn 1999b]). For species for which such precise data were unobtainable, I used a more relaxed definition for breeding seasonality: a consecutive birth season lasting less than 3 months.

The following references refer to the sources of data on SD, arboreality and breeding seasonality. Data on social organization, home range overlap, and unit size/composition are presented in Chapter 1 in this thesis.

Presbytis comata: [Plavcan and van Schaik 1997; Ruhiyat 1983]; *Presbytis siamensis*: [Plavcan and van Schaik 1997]; *Presbytis thomasi*: [Gurmaya 1986; Plavcan and van Schaik 1997]; *Presbytis potenziani*: [Plavcan and van Schaik 1997];

Presbytis rubicunda: [Plavcan and van Schaik 1997]; *Presbytis hosei*: [Rowe 1996]; *Trachypithecus obscurus*: [Nunn 1999b; Plavcan and van Schaik 1997; van Schaik et al. 1999]; *Trachypithecus geei*: [Mukherjee and Saha 1974; Plavcan and van Schaik 1997]; *Trachypithecus vetulus*: [Nunn 1999b; Plavcan and van Schaik 1997; van Schaik et al. 1999]; *Trachypithecus johnii*: [Plavcan and van Schaik 1997; Poirier 1970]; *Trachypithecus phayrei*: [Nadler et al. 2003]; *Trachypithecus leucocephalus*: [Huang and Li 2005]; *Trachypithecus pileatus*: [Plavcan and van Schaik 1997; Stanford 1991a]; *Trachypithecus françoisi*: [Nadler et al. 2003]; *Semnopithecus entellus*: [Dolhinow 1972; Nunn 1999b; Plavcan and van Schaik 1997; Smith and Jungers 1997]; *Semnopithecus schistaceus*: [Bishop 1979; Plavcan and van Schaik 1997; Smith and Jungers 1997]; *Semnopithecus priam*: [Plavcan and van Schaik 1997; Smith and Jungers 1997]; *Simias concolor*: [Rowe 1996; Tilson 1977]; *Rhinopithecus bieti*: [Grüter and Zinner 2004; Kirkpatrick 1998]; *Rhinopithecus roxellana*: [Grüter and Zinner 2004; Kirkpatrick 1998]; *Rhinopithecus brelichi*: [Bleisch et al. 1993; Kirkpatrick 1998]; *Rhinopithecus avunculus*: [Kirkpatrick 1998; Le and Boonratana 2006]; *Pygathrix nigripes*: [Hoang 2007; Nadler et al. 2003]; *Nasalis larvatus*: [Nunn 1999b; Plavcan and van Schaik 1997; van Schaik et al. 1999].

Results

Sexual dimorphism in body weight differed significantly among the modular, non-modular and multimale-multifemale species (One-way ANOVA, $F = 6.4590$, $p = 0.0065$, $df = 2$) (Fig. 2.2). Post hoc tests (Tukey HSD) showed that there are significant differences between modular and non-modular species ($p = 0.007$), but no differences between multimale-multifemale and non-modular species ($p = 0.119$) and between multimale-multifemale and modular species ($p = 0.967$).

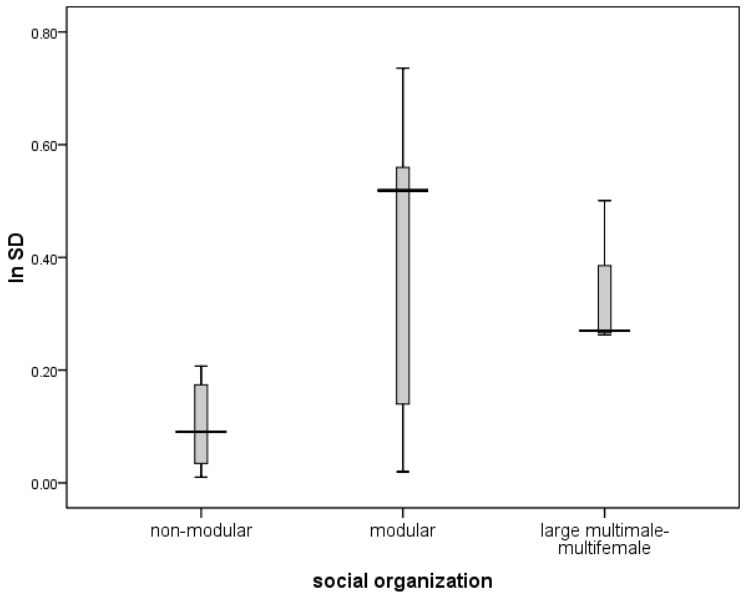


Fig. 2.2. Boxplots illustrating differences in sexual dimorphism between Asian colobine species with varying modal social organizations.

Using a General Linear Model (GLM) including other independent variables, i.e. substrate (arboreal vs. arboreal/terrestrial), unit composition (one-male vs. multi-male), and unit size, the model was significant ($F = 3.85$, $p = 0.0223$, $R^2 = 0.491$). However, of the independent variables, social organization was the only one that had a significant effect upon the response variable SD ($p = 0.0224$) (Tab. 2.2). Data on breeding seasonality are available for only 9 species, a sample too small to evaluate concomitantly the relation between SD and other variables. However, in a single regression with breeding seasonality as a predictor variable, birth seasonality did not have a significant effect on SD ($F = 1.2448$, $p = 0.3014$, $df = 1$).

Tab. 2.2. Results of GLM between each predictor variable and ln body mass dimorphism in Asian colobines.

Predictors	B	T ratio	p
Social organization (mod vs. non-mod)	0.118	2.53	0.0224
Ln unit size	0.082	0.59	0.565
Unit composition (OM vs. MM)[1]	-0.086	-1.60	0.128
Substrate (A vs. A/T)[2]	-0.035	-0.73	0.478

[1] OM = one-male, MM = multi-male.

[2] A = arboreal, A/T = arboreal and terrestrial.

If I restrict the analysis to non-modular colobines, there was no difference in SD between OM-based and MM-based species (Mann-Whitney U, $U_{2,7} = 2.00$, $p = 0.142$).

I then checked for the influence of modularity on SD by using ln home range overlap as its continuous proxy, and obtained the following bivariate regression equation:

ln SD = -0.233 + 0.144*ln home range overlap

Ln home range overlap was a significant predictor variable of body mass dimorphism ($F_{1/15} = 12.11$, $R^2 = 0.447$, $p = 0.0034$) (Fig. 2.3a). Using independent contrasts, the result was confirmed: $F = 7.12$, $p = 0.0175$ (Fig. 2.3b).

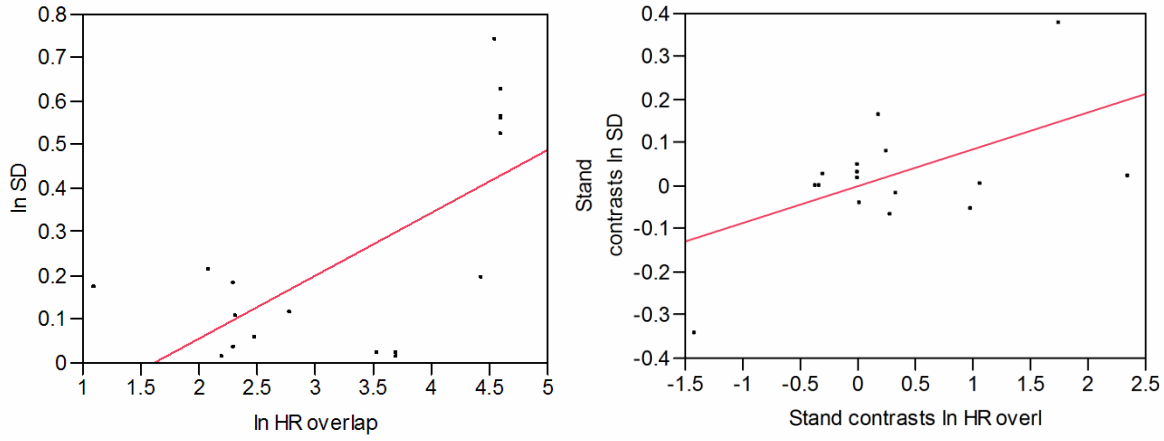


Fig. 2.3. Plots from the single regression analysis of ln home range overlap on sexual dimorphism in body mass. (a) Species values, (b) independent contrasts.

Including other independent variables, i.e. substrate (arboreal vs. arboreal/terrestrial), unit composition (one-male vs. multi-male), and unit size, the model was nearly significant ($F = 3.05$, $p = 0.0597$, $R^2 = 0.504$). Of the independent variables, home range overlap was the only one that had a significant effect upon the response variable SD ($p = 0.0485$) (Tab. 2.3).

Tab. 2.3. Results of GLM between each predictor variable and ln body mass dimorphism in Asian colobines. In this model, the categorical variable social organization is replaced with ln home range overlap, a continuous surrogate measure for modularity.

Predictors	B	T ratio	p
Ln home range overlap	0.12	2.20	0.049
Ln unit size	0.17	1.06	0.308
Unit composition (OM vs. MM)[1]	-0.05	-0.62	0.545
Substrate (A vs. A/T)[2]	-0.01	-0.17	0.865

[1] OM = one-male, MM = multi-male.

[2] A = arboreal, A/T = arboreal and terrestrial.

Discussion

Using a multivariate approach and including taxa omitted in previous analyses (such as *Rhinopithecus* spp.), I demonstrated with this analysis that social organization is the best predictor of the degree of sexual dimorphism in body weight found among the Asian colobines. My phylogenetic and nonphylogenetic results are broadly consistent, which suggests that my quanitative tests of the predictions are robust to biases due to phylogenetic history. Other variables such as substrate, unit size, unit composition and breeding seasonality did not have significant explanatory power.

Male-male agonistic competition is the mediator between sexual dimorphism and modularity. Plavcan and van Schaik [1992] formalized a competition level system to estimate male-male agonistic competition, based on the frequency and intensity of contests: *High-intensity* species are those where males are reported as intolerant of one another, where males are described as engaging in escalated combat, or where males form clear agonistic dominance hierarchies based on agonistic encounters. *Low intensity* species are those where males are relatively tolerant of one another, where agonistic encounters are rare, or where dominance hierarchies either are absent, or are difficult to detect. *Low frequency* species are those where only a single adult male typically occurs in a breeding group, agonistic competition is inevitably less frequent than in groups with more than one adult male (which were classified as *high-frequency*). In the former case, male-male competition is usually limited to occasional encounters with extra-group males, while in the latter case male-male competition can potentially occur on a daily basis. The potential frequency of intermale aggression is basically a function of the proximity of males to each other.

Following that scheme, colobines living in autonomous OMUs such as many *Presbytis* and *Trachypithecus* species were classified as level 3 (high intensity, low frequency) by Plavcan and van Schaik [1992]. They included some multilevel taxa such as *Theropithecus* and *Nasalis* in competition level 4 (high intensity, high frequency) because the continuous or frequent proximity of males, as found in nested societies, indicates high-frequency competition. I tentatively propose an amendment to the original scheme by differentiating between the multimale-multifemale *Semnopithecus* spp. with high intensity and medium frequency competition and the modular species such as *Rhinopithecus* spp. with high intensity and high frequency competition (Tab. 2.4). Even though the difference between multimale-multifemale and modular species in SD was not significant in the analysis, modular colobines tended to have higher SD than multimale-multifemale ones. When restricting the analysis to *strongly* modular species, i.e. the ones forming rather tight bands (*Pygathrix*, *Rhinopithecus*, and *Nasalis*), a one-way ANOVA with a Tukey HSD post hoc reveals that there is a significant difference in SD between modular and multimale-multifemale colobines ($p > 0.05$). The classification of Tab. 2.4 is further corroborated by preliminary field observations showing that aggressive glares and chases and avoidance between males occurred when members of different OMUs of *R. bieti* came within a few meters of each other [Kirkpatrick 1996]. In *R. roxellana*, a linear dominance order was found among unit males in a provisioned group [Tan et al. 2003; Zhang et al. 2006], indicating that male-male tolerance is low. Fights between OMUs occurred frequently, averaging 11 times a day [Tan et al. 2003].

Tab. 2.4. Scheme depicting competition levels in Asian colobines based on differing association degrees (social organizations) and the corresponding magnitude of SD.

Social organization	Body weight dimorphism (SD)	Competition level	Examples
Autonomous OMUs	Low	High intensity, low frequency (3)	Some *Presbytis* spp.
Multimale-multifemale groups	Moderate	High intensity, medium frequency (4)	Most *Semnopithecus* spp. populations
Modular societies	High	High intensity, high frequency (5)	*Rhinopithecus* spp., *Nasalis larvatus*

This study dealt only with body size dimorphism. For canine dimorphism, it has been hypothesized by Plavcan and van Schaik [1992] that, where continuous proximity and conflict of interest make escalation likely (such as in nested societies), but the cost of fighting is high to both contestants, natural selection favors the development of weaponry (i.e.

canines) for deciding the outcome of contests through display (so as to avoid frequent escalation and thus allow coexistence). Unfortunately, not enough comparable data are available on Asian colobines to conduct a thorough analysis on the relation between canine dimorphism and social organization. However, a cursory inspection of the few available data shows that the Chinese rhinopiths - all modular - have an extreme maxillary canine dimorphism that is greater than that reported for any other colobine monkey [Jablonski and Pan 1995]. Based on Plavcan et al. [2005], the species among the Asian colobines with the highest degree of canine dimorphism are *Nasalis larvatus*, and *Pygathrix nigripes*, both modular taxa. A previous study on canine dimorphism and intrasexual competition in anthropoid primates (albeit without inclusion of *Rhinopithecus*) demonstrated that most colobines show substantial canine dimorphism, with *Presbytis* being less dimorphic and *Semnopithecus*, *Pygathrix* and *Nasalis* being more dimorphic. These findings are in line with our present findings on body size dimorphism and follow the predictions of male mating contest precisely.

Dimorphism may also be a function of male coercion potential or female choice. Coercion does not seem to be important among these colobines, but female choice may be. Female choice is thought to have an impact on dimorphism in at least some anthropoids and should reinforce male reproductive skew, leading to the evolution of strong dimorphism [Plavcan 2004]. Where there is continuous risk of harassment by extra-group males, it may pay females to be with the largest possible males, because they protect them best against outside threat. In that case, the modular ones, with their permanent harassment risk by the all-male unit males [Chapters 1 and 3 in this thesis], may have experienced selection on increased male size, more so than other taxa. This hypothesis is supported by our data, both with regard to body size and canine size.

In sum, my findings provide clear support for the sexual selection hypothesis, i.e. that weight dimorphism is strongly associated with competition. Modularity or the degree of association among OMUs appears to provide an accurate indication of intermale competition in Asian colobines, missed as a significant factor in the previous analysis by [Plavcan and van Schaik 1997]. What distinguishes modular from non-modular colobines is the frequency of competition which is contingent on their respective social organisation. Modular colobines are characterized by higher frequency of competition, and this independent frequency effect influences SD in colobines. What remains unresolved is why non-modular colobines show relatively lower degrees of body weight dimorphism (but not canine dimorphism) as

compared to other anthropoids living in uni-male groups such as *Cercopithecus* spp. [Plavcan and van Schaik 1997].

CHAPTER 3 - Features of the Social System of *Rhinopithecus bieti*

Introduction

A key reason why primates are scientifically appealing is due to the fact that they show a great variety of social systems [Campbell et al. 2007; Clutton-Brock and Harvey 1977; Crook and Gartlan 1966; Dunbar 1988; Eisenberg et al. 1972; Grzimek 2004; Rowe 1996; Smuts et al. 1987], with 'social system' encompassing both grouping characteristics and the nature of inter-individual relationships [Kappeler and van Schaik 2002]. A particular social system of a given species or population results from the combined interactions of individuals [Hinde 1976], which themselves are shaped by ecological factors such as distribution of resources and predation threat [Alexander 1974; Sterck et al. 1997; Terborgh and Janson 1986; van Schaik 1983], social factors such as sexual conflict, molded by life history [Clutton-Brock and Parker 1995; van Schaik 1996; van Schaik and Kappeler 1997] and perhaps cognitive constraints [Dunbar 1992].

Among colobines, *Rhinopithecus bieti* (the black-and-white snub-nosed monkey), is an intriguing species with regard to many morphological, ecological and behavioral features. Among the natural history characteristics not shared by the majority of the colobines are semiterrestriality [Kirkpatrick and Long 1994], association with subalpine environments [Zhao et al. 1988; Chapter 4 in this thesis], semi-nomadic ranging style [Kirkpatrick et al. 1998; Xiang 2005; Chapter 5 in this thesis], a resource base made up of lichens [Kirkpatrick 1996; Chapter 7 in this thesis] and extremely large groups [Kirkpatrick et al. 1998]. Originally thought to be organized into multifemale-multimale groups [Bai et al. 1987; Li et al. 1982; Wu 1993; Yang 1988], preliminary work has provided evidence that *R. bieti* societies are organized in small monandrous-polygynous subunits (one-male units or OMUs), which almost permanently conglomerate into well-organized larger and relatively cohesive bands [Cui et al. 2008; Kirkpatrick et al. 1998; Liu et al. 2007], with all-male units being part of these bands as well. This social arrangement with two rather fixed layers is referred to as a nested society [Grüter and Zinner 2004, Chapter 1 in this thesis]. Social behavior in *R. bieti* has received relatively scant attention [Grüter 2003; Kirkpatrick et al. 1998]. Almost nothing is known about the bonding pattern that characterizes the *R. bieti* social units. Kirkpatrick et

al. [1998], in a pilot study, found that intra-unit aggression is infrequent and grooming is relatively frequent as compared to other Asian colobines. Moreover, grooming episodes involved both sexes, with an overrepresentation of females.

The collection of basic data on group size and composition is not straightforward in this species because of extremely large groups, low levels of habituation and restricted visibility in the natural environment. Group composition data of *R. bieti* have been derived from eyewitness accounts and video analysis of groups crossing open land [Cui et al. 2008; Liu et al. 2007], scrutinizing faeces dispersed at sleeping sites [Cui et al. 2006b], and direct scan observations with telescopes of group members staying in the canopy [Kirkpatrick et al. 1998]. Here I use a relatively large data set stemming from a free-ranging semi-habituated group that was followed for a period of 20 months. The study was set up with several objectives:

1) To provide basic demographic data on *R. bieti* group size and composition.
2) To deepen our understanding of the multilevel structure of *R. bieti* societies and provide quantified analysis (previous descriptions have remained primarily qualitative). This is done by determining spatiotemporal distribution of individuals and OMUs in the band. I made the following predictions for the existence of multilevel societies:
    a. The identity of the nearest adult neighbor of a scanned individual is strongly female-biased in modular societies as opposed to multimale-multifemale groups where the sex of the neighbor is closer to random.
    b. OMUs do not share patches (trees), so the maximum number of males per tree is 1.
    c. The temporal arrangement of males in the marching band follows an even distribution in case of a modular organization and a random or even clumped distribution in case of a multimale-multifemale organization.
3) To evaluate the possible existence, time frame and determinants of fission-fusion events.
4) To better understand the social mechanisms by which OMUs are held together by studying the quality and quantity of social interactions and spatial arrangements among age-sex classes. If proximity and grooming reflect social affiliation and relationships [Dunbar 1991; Kummer 1971; White and Chapman 1994], we hypothesize that males in ‘crowded’ modular systems, where maintaining social

integrity of the unit is vital, males would be socially integrated into the unit, i.e. would be involved in the grooming network and spend time in proximity with other unit members, unlike most other Asian colobines (Kirkpatrick 2007).

5) Moreover, I assess the functional basis of allogroomong in colobines, i.e. whether the frequency of grooming among different species is related to group size (the social hypothesis) or substrate (the hygiene hypothesis). Dunbar (1991) and Lehmann et al. (2007) found for primates in general that time spent grooming is positively correlated with group size and argued that this is because animals in larger groups need to invest more time servicing social relationship to maintin group cohesion. Majolo et al. (2008) in contrast, did not find statistical evidence that time spent on grooming is affected by group size in primates. A correlation between grooming and substrate would provide support for the hygiene hypothesis because a terrestrial lifestyle involves increased contact with ectoparasites such as ticks, leeches and dirt and would require a greater amount of allogrooming.

Methods

Study site

The study site, Samage, is located at 27°34'N, 99°17'E in the Baimaxueshan National Nature Reserve, Yunnan, PR China (Fig. 3.1). The area is dominated by steep mountain slopes and narrow ravines covered with a mosaic of mostly temperate vegetation types: mixed coniferous and deciduous-broadleaf forest (at 2900-3600 m), sub-alpine George's fir forest (3500-4000 m), montane sclerophyllous oak forests (3200-3500 m), subtropical evergreen broadleaf forest (2500-3000 m), Yunnan pine forest (2500-3100 m), alpine scrublands (3700-4100 m) as well as cattle pastures at various elevations. The area is demarcated to the north by the border between the counties of Weixi and Deqin. Parts of the Samage Forest have been selectively logged, and human encroachment in the form of livestock grazing and harvest of forest products is widespread. The habitat of snub-nosed monkeys at this locality ranges from 2500 m to 4000 m and includes all major vegetation types, but predominantly mixed forest. The site experiences extreme seasonal variation in precipitation and temperature. Monthly temperatures at base camp ranged from a mean of 6.6° in January 2007 to a mean of 21.5° in July 2006, and monthly amount of precipitation (rain or snow) from 0

mm in January 2006/2007 to 275 mm in August 2007. A more detailed ecological description of the site is given in Chapters 4 and 7 in this thesis.

Fig. 3.1. Location of the study site at the southern extremity of the Baimaxueshan Nature Reserve in Yunnan, China. Map by K. Meisterhans.

Data Collection

During the 20-month study period (Sep 2005 – May 2006; Aug 2006 – Nov 2006; Jan 2007 – Jul 2007), the not yet fully habituated focal band (the Gehuaqing band) was located on 315 days, with total contact time of 1444 h (Tab. 3.1). Behavioral data were collected on 116 of these days. The number of scan-based visual contact hours was 456 during which 19,146 individual activity records were collected. Using a high-performance spotting scope (Kowa® TSN 820, 20-60x Zoom), behavioral observations were usually conducted from rocky outcrops, ridges or hillsides. These distance observations ensured that the animals were unaware of the observer's presence and allowed me to obtain a better overview of the spatial configuration of the group members and see into forest patches that were difficult to reach on

foot. However, group members now and then accepted me to stay within 10-30 m to them. Taken as a whole, distances to the location of the monkey group ranged from 10 to 1,500 m (mean: 240 m +/- 211 m; median: 200 m). I was only rarely able to re-identify a given OMU. Only very few individuals could be repeatedly recognized by conspicuous traits, e.g. a split lip, a damaged eye, or a missing limb.

Tab. 3.1. Contact time with the *R. bieti* group at Samage between Sep 2005 and Jul 2007.

Month	Days with contact[1]	Contact time (h)[2]	Days with scans	Scan-based contact time (h)
Sep-05	9	27.5	6	20
Oct-05	10	53.5	7	37
Nov-05	7	38	7	22.25
Dec-05	14	45	9	28.75
Jan-06	4	20	2	7
Feb-06	6	21	1	8
Mar-06	12	60	8	34.25
Apr-06	16	62	6	26.5
May-06	12	44.5	5	21.5
Jun-06	9	26.5	0	0
Jul-06	14	41.5	0	0
Aug-06	17	51.5	6	16
Sep-06	30	252.5	6	31.25
Oct-06	15	54	8	22.75
Nov-06	15	65	6	30.25
Dec-06	15	19	0	0
Jan-07	20	134	5	23
Feb-07	9	32	5	16.5
Mar-07	12	30	4	15.75
Apr-07	22	146.5	10	31.5
May-07	14	47	4	18.25
Jun-07	14	39	5	22.25
Jul-07	19	134	6	22.75
Sum	315	1444	116	455.5

[1] Contact by CCG and assistants.

[2] Visual and audible contact.

Systematic data on social behavior were collected via scan sampling [Altmann 1974; Morrison et al. 1998] of the focal group. Scans of all visible animals were taken at 15 min or 30 min intervals and dictated into a tape recorder. Group members were often spread out over large distances (mean: 130 m +/- 110 m; median: 90 m) in the forest and across forest strata, precluding data collection on all members of the group during a single scan. Animals on the ground were frequently overlooked during scans due to poor visibility. If a large number of monkeys (usually >20) was in view, I chose 30 min scans; if only a small number (usually <20) was visible, I did 15 min scans. Scans needed to be completed at least 5 min before the

beginning of the next scan. Every scan included information on date, time and weather conditions. For every subject being scanned, I recorded age, sex, activity (rest, groom, move, play, feed, vigilance, cling, aggressive, and miscellaneous). I also recorded the distance to nearest neighbor (in arm's lengths), age-sex class of nearest neighbor and recorded all animals occupying the same tree. For definitions of activity categories, see Appendix 1 to this chapter. Both sexual and aggressive behavior including display behaviour (visible and audible; in the latter case judging from loud fighting call) was scored *ad libitum*.

Age/sex classes are divided into the following categories: adult male, adult female, subadult male, juvenile (ca 1-4 yr), and infant (<1 yr). The individual was recorded as 'unclassified' if age/sex class could not be recognized. Subadult males in snub-nosed monkeys are sometimes falsely identified as adult females [Bleisch et al. 1993]. I thus used the category 'SAMOF' (subadult male or female) for cases where it was not possible to determine the sex of an animal whose body size was close to or bigger than that of an adult female, but was not accompanied by an infant. Appendix 2 to this chapter lists the morpho-behavioral criteria used to distinguish apart the age/sex classes in *R. bieti*. Because the birth season is March/April (see below), infants were recognized until February of the next year; after that, they were treated as yearling juveniles.

The density of the forest canopy and underbrush coupled with the semi-terrestrial lifestyle of the monkeys prevented me from obtaining reliable group counts during scan sessions. Occasionally, however, I had the opportunity of observing the band crossing an open area (gully or a ridge) at rather close range (<100m), allowing me to obtain an accurate count of all members of the group. One such group progression (Nov 12, 2006) was also filmed, but not completely. Fission-fusion was studied by more or less simultaneously following two group parts and taking GPS coordinates. For details on how I sampled geographical positions of the group, see Chapter 5 in this thesis.

Data Analysis

Scan records were used to generate summary data on time spent in proximity to others for each age-sex class, distance and identity of the nearest neighbor, time spent grooming, identities of groomer and groomee and demographic composition of the band. I excluded unclassified individuals from calculations of age-sex composition. All individuals recorded as 'adult female or large juvenile' were treated as adult females for demographic analyses. Data on OMU size and composition are not provided because I had no *a priori* criterion for

differentiating among OMUs, and because rarely all suspected OMU members were visible to the observer due to thick foliage occluding clear lines of sight.

The video footage showing a part of the group crossing a gully on Nov 12, 2006 was analyzed on screen: I recorded the time intervals between successively passing individuals. Time intervals reflect proximities and were used to detect social boundaries between age-sex classes. A one-sample runs test [Siegel and Castellan 1988] was used to ascertain whether the arrangement of males and females in the moving column was random. Seasonal rates of aggression were analyzed by one-way ANOVA. Prior to conducting the ANOVA, I checked the data for homogeneity of variances using Levene's test and for normal distribution using a one-sample KS test.

For the comparative analysis of grooming frequencies in different species of Asian colobines, I used a General Linear Model (GLM) to simultaneously assess the effect of several predictor variables (substrate, group size) on the dependent variable (percentage of grooming). To comply with normality, group size was natural log transformed and petrcentage of grooming was arcsine square root (angular) transformed. The data on grooming frequency and substrate use are the same as in Chapter 1 in this thesis with one new datum on *Presbytis thomasi* (van Oijen 1992). Analyses were run in JMP 7.0.2 (SAS Inc.) and SPSS 16.0. All probabilities reported are for two-tailed tests. Statistics were considered significant at $p < 0.05$.

Results

Group Size and Composition

Based on the whole group progression on June 17 2007, the total number of individuals counted in the focal group was 407. Due to the high possibility of having missed some individuals taking a different travel path, this is a minimum estimate. The adult male-female ratio was 1:2.2 (Tab. 3.2). When I restricted the demography estimates to the putative reproductive population [Kirkpatrick and Gu 1999] and excluded 17 males that moved along tightly with other adult or subadult males and presumably were part of bachelor units, the sex ratio then became even more female biased (1:3.0). The ratio of adult females to infants was 1:3.3.

As a complementary measure to this group count, I determined sex ratios based on the frequency distribution of age/sex classes in scans (n_{fem} = 4,539, n_{mal} = 2,516, n_{juv} = 4,379, n_{inf} = 1,443). The male-female ratio was 1:1.8 and the ratio of adult females to infants was 1:3.2. The estimate derived from the direct census is likely more accurate than the scan-based one since adult males were consistently more conspicuous and more easily detected than females.

Tab. 3.2. Demography of the Gehuaqing group of *R. bieti* at Samage, as estimated from a group census on June 17, 2007.

Number							Ratios	
Male	Female	Juvenile	Infant	SAMOF	Unk	Tot	M:F	I:AF
63 (46*)	138	132	42	21	11	407	1:2.2 (*3.0)	1:3.3

* Excluding putative non-reproductive AMU males.

By plotting the time intervals between sequentially passing adult and subadult males, it became evident that there were clear temporal gaps between males (Fig. 3.2). Males were more clumped only at the periphery, representing the AMUs that led the progressions. After excluding the AMU males (n = 15), I used a one-sample runs test to determine whether the arrangement of males and females in the moving column was random (infants and juveniles and were not considered in this analysis because infants did not usually walk independently and juveniles were both associated with OMUs and AMUs). The order was not random (r [number of runs] = 46; n_{mal} = 23, n_{fem}= 86, z = 2.38, p = 0.014, two-tailed), with the large number indicating that adult males were overdispersed.

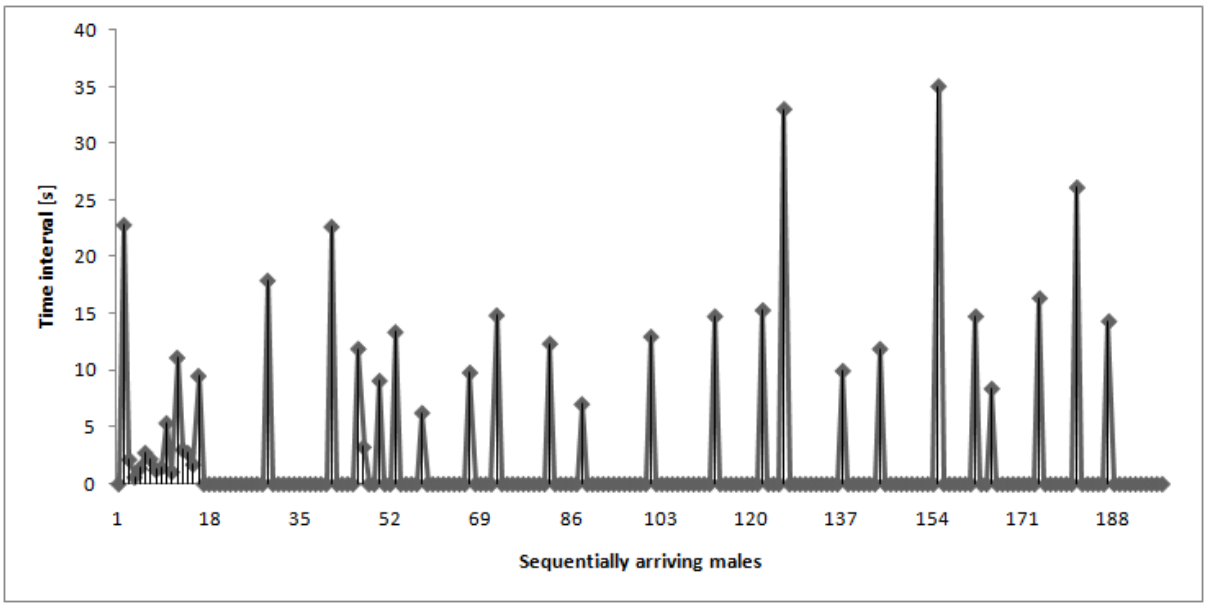


Fig. 3.2. Time interval between arriving adult and subadult males (based on the video footage of a partial group progression on Nov 12, 2006). The diamonds on the x axis refer to females and juveniles.

How group movement was initiated, how travel direction consensus was reached and how travel is coordinated is still unclear, but the rate of vocalizing constantly increased before moving. All OMUs used the same travel path and sometimes formed parallel walking columns (sometimes a single column moving terrestrially). On two occasions I saw a single male moving in front and one in the rear, 'temporally separated' from the band by 30 s up to a few minutes.

One-male units were the core units of the *R. bieti* society and are composed of one male, an assumed average of 3 adult females (based on the population-based sex ratio) and a not quantified number of adolescents. One-male units also appeared to monopolize valuable feeding trees. Units appeared to tolerate each others' presence/neighborhood, but adult members typically did not interact obviously. When members of different units came to within a few meters of each other, aggressive gestures and vocalizations were common. Obtaining correct data on mean OMU size have proven difficult due to the fact that rarely all OMU members were clearly visible in trees and an unambiguous differentiation among OMUs was not possible. We have only a few cases of more than one male (n = 18; 1.14% of tree scans), but several females, staying in the same tree during siesta periods (AMUs excluded; n = 166; 10.51%), so OMUs seem to be cohesive units that stay together in only one single tree and keep a spatial distance from other units (Fig. 3.3). Derived from the number of individuals staying in the same tree, the largest OMU had 17 members (1 male, 8 females, 5 infants, 3 juveniles).

Fig. 3.3. An OMU with an adult male in the center and 2 females with infants, 2 juveniles and one unidentified individual surrounding him. OMU members tended to stay closely together while resting. Photo © J. Weingarten.

All-male units (AMU) or bachelor units are another element within the *R. bieti* society. There were two kinds of all-male units, adult-male units (AAMU) and subadult male units (SAMU) and mixed adult-subadult units. SAMUs were made up mostly of large male juveniles and subadult males. AMUs usually contained adult males. The size of all-male units varied over time (mean 4.99, SD 3.43; range 2-17; median 4). The largest AMU with 17 members was composed of 4 adult males, 8 subadult males, and 5 juveniles. One suspected AMU had 33 members (a few individuals could not be reliably sexed). On a few occasions, we saw pairs or lone males wandering around separately from the main band, at distances >1 km. AMU males showed affiliative behavior towards each other: they occasionally groomed and mounted each other. AMU members often exhibited stereotyped displays: they rushed through the canopy, stopped abruptly and then remained in a semi-crouching position for a few seconds before rising ('jumping and freezing'). AMUs were seen on 62 days, i.e. 53% of all observation days. We recorded the position of AMUs in relation to the most peripheral OMUs, i.e. whether they were peripheral (>500 m), close to (200-500 m) or inside the group (<200 m). Usually they did not stay far away from the main band, but tended to be close to the family units (Fig. 3.4). Sometimes they were seen in the center of the band within reach of the OMUs. On the 47% of days on which we did not see the AMUs, they may have been peripheral.

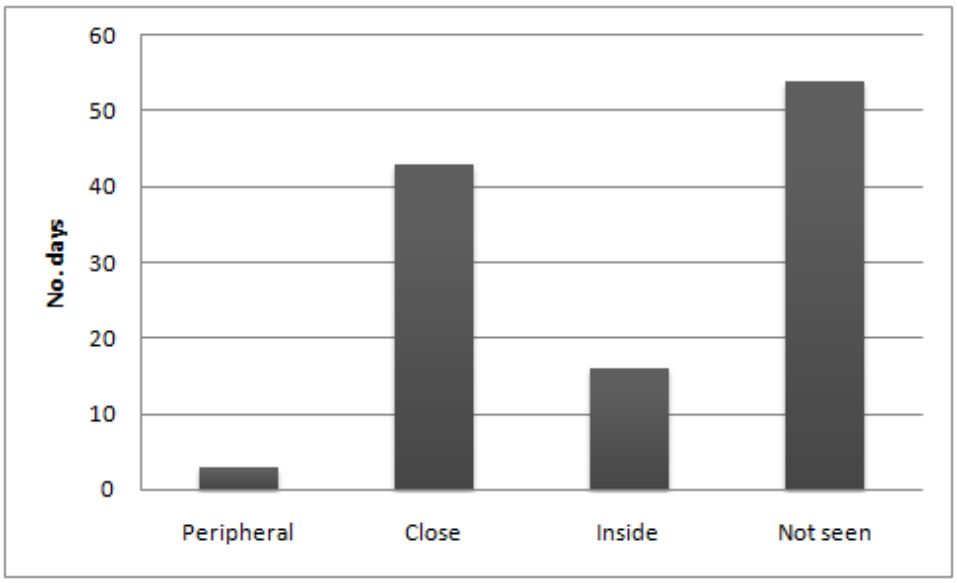


Fig. 3.4. Position of AMUs in relation to OMUs. 'Peripheral' is >500 m, 'close' is 200-500 m, and 'inside' is <200 m.

Fission-fusion

My impression is that the study group of *R. bieti* was relatively stable and unified. The group sometimes broke up briefly for several hours as a result of logistics of travel, food distribution, or human disturbance. Sometimes local cattle herders cut off the group's way, resulting in one part staying on one side of the ridge, and the other on the other side. The subgroups usually assembled again in the evening. Only once was I able to document a long-term group fission: two splinter groups of several one-male units were observed traveling separated from each other for several weeks in late winter, separated by a maximum of >5 km (Fig 3.5.).

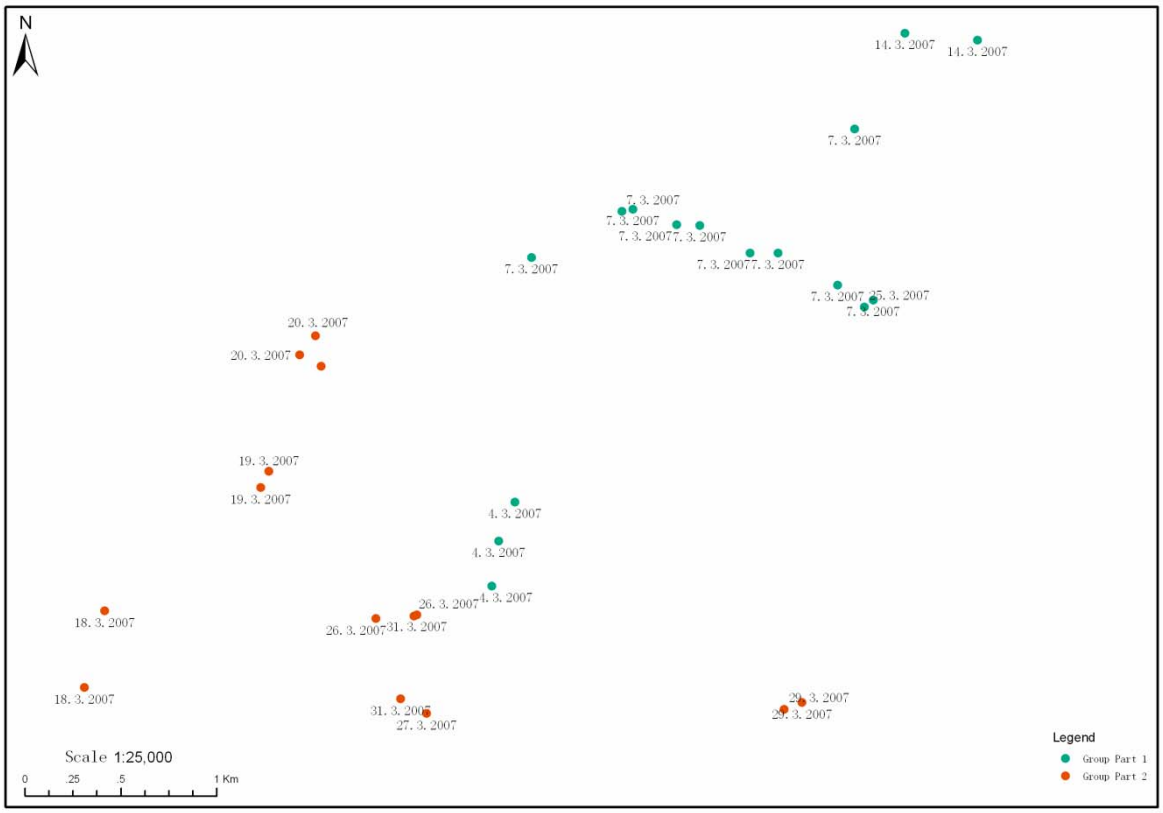


Fig. 3.5. A fission event of the study group in March 2007. The red points indicate the locations of one splinter group, and the blue points the locations of the other. The dates (d/m/y) on which the location records were obtained are also given.

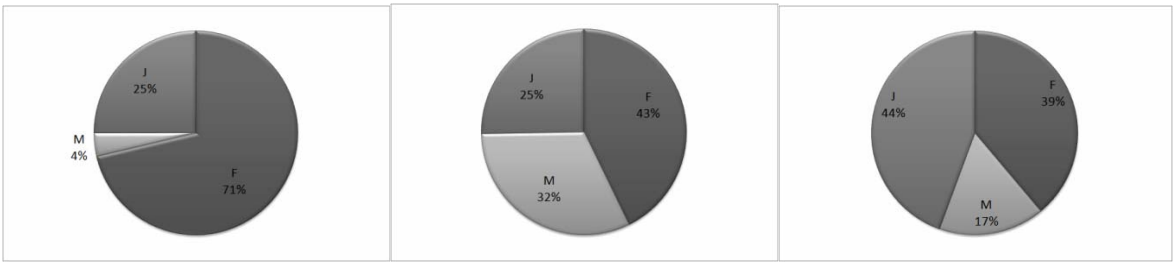
Spatial and Social Behavior

Adult females were seen in proximity (<1 arm's length) with another unit member on 31% of all scans, males on 21%, juveniles on 20% and infants on 61%. This analysis was restricted to OMUs and to times when the animals were not moving. The actual values are likely higher because it was sometimes difficult to see if a scanned animal was in fact in body contact with another one when rest-huddling. The comparison among age/sex classes however still remains valid since this bias is inherent and affects all age/sex classes equally.

Different age-sex classes varied in their nearest neighbor and proximity relations. As measured by the identity of the nearest neighbor (Fig. 3.6), males had females as nearest neighbors much more often than expected (the expected percentage was determined from the composition of the study band), and other males and juveniles much less often ($\chi^2 = 284.542$, $df = 2$, $p < 0.001$) (Fig. 3.6a). Females had other females as nearest neighbors about as often as expected, males more often and juveniles less often ($\chi^2 = 510.510$, $df = 2$, $p < 0.001$) (Fig.

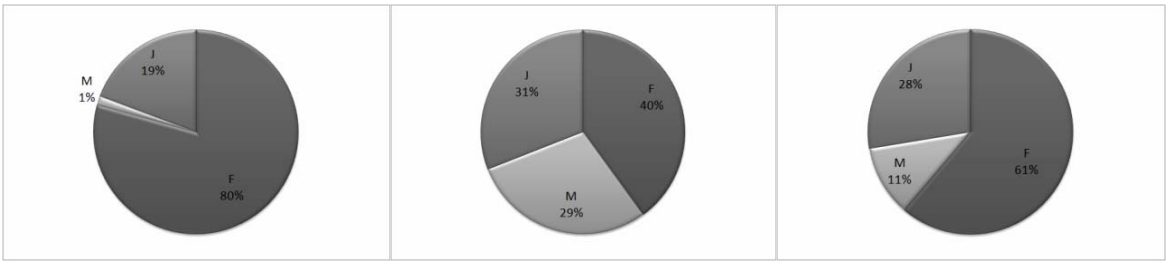
3.6b). Juveniles had females as nearest neighbors less often than expected, other juveniles and males more often (χ^2 = 14.563, df =2, p = 0.001) (Fig 3.6c).

When considering the identity of the animal in proximity, results are similar (Fig. 3.7). Males were in proximity mostly with females (80%) and very rarely with other males (1%) (Fig. 3.7a). Females showed proximity with all age-sex classes at comparable frequencies (Fig. 3.7b). The nearest neighbor and proximity diagrams look very similar for females and males, but differ for juveniles: while other juveniles were most often nearest neighbors of juveniles (44%), it was most often females who stayed in proximity with juveniles (61%) (Fig. 3.7c).



(a) (b) (c)

Fig. 3.6. Identity of nearest neighbors: the (observed) percentage of time for which an individual of a particular age/sex class was nearest to the subject. (a) Male, (b) female, (c) juvenile.



(a) (b) (c)

Fig. 3.7. Identity of animal in proximity (<1 arm's length). (a) Male, (b) female, (c) juvenile.

The snub-nosed monkeys spent 6.7% of their diurnal activity budget in allogrooming. After excluding SAMOF and infants from the χ^2 analyses, the observed frequencies of active allogrooming differed significantly from the expected ones based on the relative representation of these age/sex classes in the group (chi square goodness of fit, χ^2 = 112.478, df = 2, p < 0.001), i.e. males and juveniles groomed less than expected and females more than expected (Tab. 3.3). The observed frequencies of passive allogrooming also differed significantly from the expected ones (χ^2 = 50.180, p < 0.001, df = 2), i.e. females were groomed about as often as expected, while males were groomed more than expected and

juveniles less than expected (Tab. 3.3). Females groomed other females, males and juveniles at about equal frequencies whereas males groomed mostly females. Females received grooming by all age-sex classes, but most often by other females. Males received grooming predominantly by females. Grooming bouts often lasted several min, though the sampling regime did not allow me to record actual duration.

Tab. 3.3. Grooming dyads (n = 449) within *R. bieti* OMUs. Grooming episodes within AMUs are not considered here.

		GROOMEE						
		AM	AF	J	I	SAMOF	TOT	%
GROOMER	AM	0	34	2	0	3	39	9
	AF	68	87	89	58	0	302	67
	J	26	39	21	6	6	98	22
	I	0	1	0	0	0	1	0
	SAMOF	6	0	0	0	3	9	2
	TOT	100	161	112	64	12	449	100
	%	22	36	25	14	3	100	

Only 4 copulations were witnessed in ca 500 hours of direct observations, with 1 in late summer, 2 in the fall and 1 in early winter. Newborn infants were observed from March to April, in both 2006 and 2007. With a gestation length of ca 7 mo (He et al 2001), conception is assumed to happen in Aug-Sep, coinciding with more frequent copulating.

Since aggressive behavior was difficult to record visually, I used aural cues, i.e. the characteristic male aggressive calls, as an indicator of an aggressive event involving a male. I compared the number of aggressive events involving males among seasons and found that hourly aggression rates involving males differed significantly among the 4 seasons (ANOVA, $F = 4.149$, $p = 0.010$, $df = 1$) (Fig. 3.8), with the highest rates in summer and fall, i.e. during the mating season. However, no statistical difference in male mating frequency between the 'conception season' and 'non conception season' was found (ANOVA, $F = 0.004$, $p = 0.954$, $df = 1$). Summer and fall are also the time of high availability of fruit, a contestable resource. I checked for a correlation between frequencies of male aggression and monthly fruit availability: for the first study year, the correlation was significant ($r_s = 0.632$, $p = 0.050$, n = 10 mo); for the second study year, the correlation was nearly significant ($r_s = 0.560$, $p = 0.073$, n = 11 mo). Finally, I investigated whether there is a statistical influence of bachelor presence on male aggression rates, with an ambiguous outcome: for the first study year, there was a highly significant correlation between monthly male aggression frequencies and the percentage of band contact days on which AMUs were seen ($r_s = 0.828$, $p = 0.003$, n = 10

mo), but not for the second year (r_s = 0.051, p = 0.897, *n* = 9 mo). If I lump all 19 months together for which these data are available, there is a trend toward a positive relationship between the two variables (r_s = 0.431, p = 0.065, *n* = 19 mo).

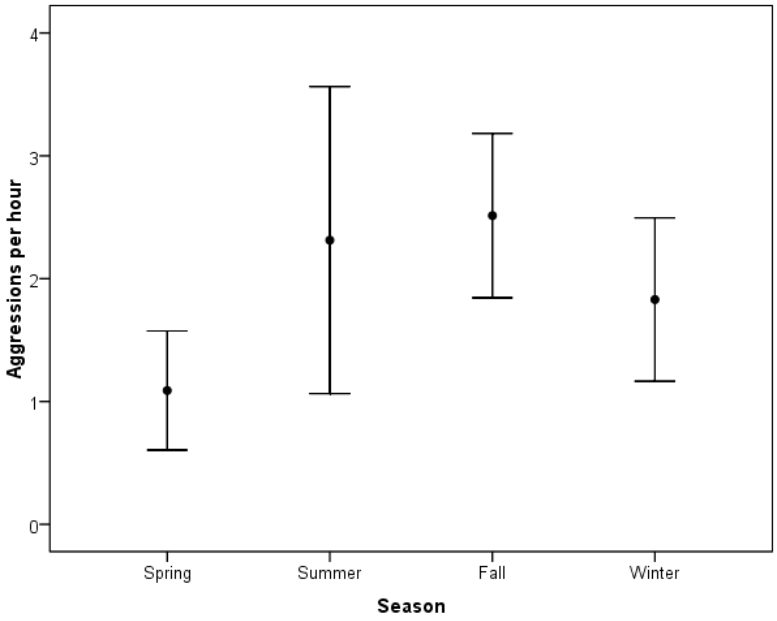


Fig. 3.8. Male aggression frequencies (no. aggressive vocal events involving males per hour) compared among seasons (spring = Mar-May, summer = Jun-Aug, fall = Sep-Nov, and winter = Dec-Feb). The means are represented by filled circles and the whiskers indicate the 95% confidence interval for the mean.

Juveniles at times provided alloparental care to infants (holding, grooming or carrying them). Males were very tolerant of infants, but usually did not engage in active caretaking/babysitting.

Grooming Behavior Compared among Asian Colobines

Data on the percentage of time spent in grooming for various species of Asian colobines are shown in Fig. 3.9. A GLM that simultaneously assessed the effect of the two independent variables group size and substrate on percentage of grooming was found to be significant (F = 8.7125, p = 0.0031, R^2 = 0.537). Of the independent variables, substrate had a significant effect on grooming (0.0357), while there was only a trend for group size (0.0656).

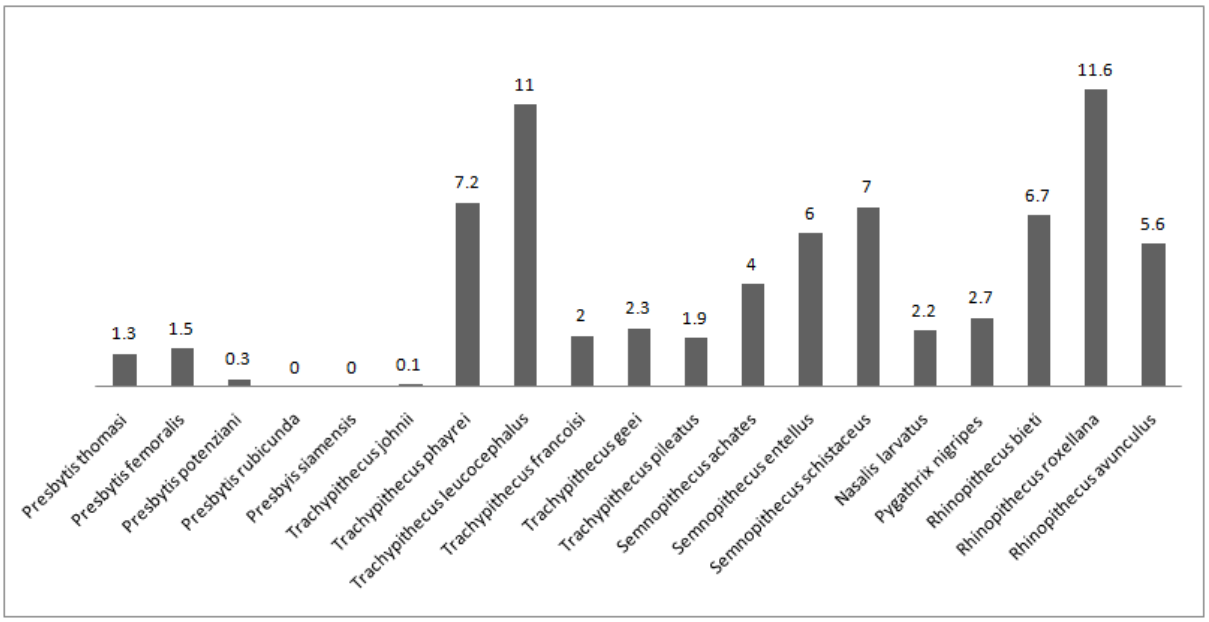


Fig. 3.9. The percentage of time spent in grooming for various species of Asian colobines. Data based on Chapter 1 in this thesis.

Discussion

Overall Group Composition and Socio-spatial Organization

My study group of *R. bieti* was formerly estimated to comprise about 200 individuals, probably based on information given by local rangers [Ding et al. 2003; Xiao et al. 2003]. It took me a year and a half of field research to work out the approximate size of the focal band. My results demonstrate that the size of the group is more than twice the original estimate, implying that the total population of *R. bieti* is larger than previously thought. Groups of more than 200 have been reported only in a small number of primate taxa: Guinea baboons (*Papio papio*) [Sharman 1981], drills (*Mandrillus leucophaeus*) [Gartlan 1970; Wild et al. 2005], mandrills (*Mandrillus sphinx*) [Abernethy et al. 2002]), Angolan black-and-white colobus (*Colobus angolensis*) [Fashing et al. 2007b], hamadryas baboons (*Papio hamadryas*) [Kummer 1984], and gelada baboons (*Theropithecus gelada*) (Dunbar 1984). Most of these are subdivided into smaller modules, indicating that such huge group sizes are incompatible with any other social organization such as multimale-multifemale groups (although the societal structure of some species is data deficient) [Grüter and Zinner 2004].

Previous researchers of *R. bieti* societies have mistakenly considered an aggregation of independent OMUs as one big multimale-multifemale group [Ma et al. 1989]. My research has provided several lines of evidence indicating that groups are organized in a modular fashion with distinct social clusters (OMUs) embedded within a band. First, an analysis of the marching formation of the band revealed that there were visible spatial gaps between males and males were evenly distributed across the whole band (with the exception of the peripheral AMU males). If it was a macaque-like multimale-multifemale group, I would expect the spacing of the males to be more random. Second, that in only 1% of the observations another male was the nearest neighbor of a focal male is clear evidence that we are not dealing with a classical multimale-multifemale group here, but with a multilevel society of discrete core OMUs united in bands. Third, using spatial distance as the judgment of social unit, we found that OMUs occupied fixed spaces and unit members maintained close proximity while resting. Trees seem to act as natural barriers separating OMUs, with one OMU usually occupying a single tree or occasionally two adjacent trees with overlapping crowns (cf. [Cui et al. 2006c; Qi et al. 2004; Ren et al. 1998]. In only 1% of the tree scans was there more than one male staying in the same tree during siesta periods (AMUs excluded) which supports my prediction that they form multilevel societies. In two other studies, only once was there more than one adult male seen in the same tree with females [Kirkpatrick 1996; MacLennan 1999]. Based on the empirical evidence that OMUs are well delineated spatially (especially obvious when resting) and more interactions occur within this social entity than between (see below), a useful criterion for allocating individuals to units would be to consider all animals within a tree as grouped, i.e. belonging to the same OMU. This recalls ecological patch theory which defines a patch as an area of food concentration such as a single tree separated from other patches by areas with little or no food [Astrom et al. 1990; Snaith and Chapman 2005].

The multi-tiered system of the *R. bieti* population at Samage appears to be basically similar to that found in other populations of *R. bieti* [Cui et al. 2008; Kirkpatrick et al. 1998] and other members of the genus *Rhinopithecus* (*R. roxellana*: [Ren et al. 1998; Zhang et al. 2006]; *R. brelichi*: [Bleisch and Xie 1998]; *R. avunculus*: [Boonratana and Le 1998]) and bears some striking resemblance to the system of proboscis monkeys [Murai et al. 2007; Yeager 1991a]. All these studies reported spatially and socially distinct OMUs that frequently or permanently stay in close proximity with other such units. On the surface, the *R. bieti* social system can also be considered as analogous to that found in gelada baboons [Dunbar and Dunbar 1975; Grüter and Zinner 2004; Kawai et al. 1983] and hamadryas baboons

[Grüter and Zinner 2004; Kummer 1968; Swedell 2006] where in both cases a multilevel society based on harems has been described. However, the latter two species differ fundamentally in many characteristics of their finer social structure such as dispersal patterns, grooming networks and harem-building strategies (*ibid*).

My demographic findings of the Samage band are largely in accordance with the Wuyapiya band [Kirkpatrick et al. 1998]. The Wuyapiya band was composed of 15-18 OMUs, with the largest putative OMU having 14-16 individuals, of which 5-6 were females. The Nanren group, which is likely identical with the Wuyapiya group, was composed of 17-29 OMUs (depending on the year of assessment and number of units sampled), with OMUs having an average size of 7.1-9.7 members of which 3.8-5.1 were females. The most conclusive count of the Tacheng group with 24 reproductive units revealed that OMUs had an average of 11.3 members and 4.7 females. The Bamei group comprised 14 reproductive/bisexual units; these units were comparatively smaller with an average of 5 individuals and 2.8 females. Overall, the population based sex ratio of *R. bieti* is around 1 male to 3 females (Tab. 3.4) at most sites, but OMU based ratios are usually higher (up to 5 females). This difference in sex ratio is likely due to an inclusion of some males associated with AMUs in the population-based estimate.

In line with Kirkpatrick et al. [1998] and Cui et al. [2008], the relatively high ratio of adult females per infant (among the highest for Asian colobines [Kirkpatrick 2007]) in this population suggests low birth rate (low female fecundity) or high infant mortality. Assuming an even sex ratio at birth, the surplus of females (even after controlling for AMU males) may be due to earlier maturation of females [Ohsawa and Dunbar 1984] or higher mortality among males [Rajpurohit and Sommer 1991].

Previous studies reported the existence of the occasional monogamous units and MMUs (multi-male units) in *R. bieti* [Cui et al. 2008; Liu et al. 2007; Xiang 2005]. However, I was unable to provide unequivocal evidence with regard to the existence of such units. On a few occasions, I saw 2 males in one tree accompanied by a cluster of females, which could be an MMU. However, when 2 males were spatially separated within the tree (e.g. one male in the upper canopy, one in the lower canopy), they may have belonged to 2 independent OMUs. I had the impression that if a tree was very tall, a second unit may have settled in the lower canopy. Given the high number of supposedly non-AMU males in the local band (46), it is to be expected that a few units contained additional males.

In some primate populations, group size is positively correlated with habitat quality [Dunbar 1987; Struhsaker 2000], supposedly because primates can maintain higher reproductive rates in high-quality habitats [Dunbar 1987]. Depending on the altitude and latitude, *R. bieti* populations occur either in predominantly mixed forest or predominantly coniferous forest. Based on the data given in Tab. 3.4, the mean group size is not different between the two habitats (Mann Whitney U, $U_{5,6} = 6$, $p = 0.099$). Using altitude as a proxy for productivity, there is also no significant correlation between band size and altitude ($r_s = 0.342$, $p = 0.452$, $n = 7$). One possible reason for the absence of an effect of habitat quality on group size is that hunting and forest destruction/compression have been particularly severe in some of the southern areas with mixed forest, thus leading to smaller group sizes despite productive habitat.

Tab. 3.4. Size, composition and habitat association for several bands of *R. bieti*. Only newest data for particular groups are given.

Study site	Main habitat	Altitude [m]	Band size	Adult sex ratio ♂ : ♀	Reference
Samage (Gehuaqing)	Mixed	3218	407	1 : 3.0[c]	This study, Chapter 4 in this thesis
Xiangguqing (Tacheng)	Mixed	3200	366	1 / 3.3[c]	[Liu et al. 2007]
Wuyapiya[a]	Conifer	4080	175	1 / 3.1[c]	[Kirkpatrick et al. 1998]
Bamei	Conifer		73	1 / 2.8[b]	[Cui et al. 2008]
Nanren[a]	Conifer		225	1 : 3.8[b]	[Cui et al. 2008]
Jinsichang	Mixed	3500	180	-	[Ren et al. 2008]
Fuheshan	Mixed	3105	80	-	[Liu et al. 2004]
Xiaochangdu	Conifer	4031	>210	1 / 2.2[c]	[Xiang 2005]
Zhina	Conifer		Ca 50	-	[Xiang et al. 2007b]
Milaka	Conifer		Ca 50	-	[Xiang et al. 2007b]
Longmashan	Mixed	3024	>80	-	[Huo 2005]

[a] This might be the same band of *R. bieti*.

[b] OMU-based estimates.

[c] Population-based sex ratios.

All-male Units

All-male units are universally associated with *Rhinopithecus* multilevel societies [Grüter and Zinner 2004]. When population density and feeding costs associated with group living are low (as is the case with most *Rhinopithecus* populations), surplus males probably fare best when joining together instead of drifting away by themselves. It remains unclear, though, whether they form alliances and in so doing gain strength and improve their chances

of success during a group takeover, as reported for hanuman langurs [Hrdy 1977]. While males of different units never engage in sociopositive behavior [Kirkpatrick et al. 1998; this study), amicable interactions exist among AMU members (cf. [Robbins 1996; Zhao and Pan 2006]), due to the absence of females and mating competition.

All-male groups were encountered on many occasions and they tended to lag behind or walk in front of the bisexual band, often at a certain distance [Bleisch et al. 1993; Liu et al. 2007; this study]. Even though they seem to be socially and spatially rather peripheralized, AMUs were sometimes seen in the center of the bisexual band [Kirkpatrick and Gu 1999; this study]. This closeness may enhance the AMU males' familiarity with the males and females of the reproductive units and may facilitate a possible later takeover attempt. This may be a similar situation as reported for zebras, where AMUs stay close to breeding units and can thereby learn how to behave toward females to later initiate and maintain bonds with them. These are social skills that can only be learned when consistently being within reach of the reproductive units, and these skills are needed for successful transition from non-breeder to breeder [Rubenstein and Hack 2004].

The few solitary males encountered were probably postreproductive males whereas most juvenile and subadult males (positively categorized from genital anatomy) as well as full-grown males found in bachelor groups were probably prereproductive (cf. [Bleisch and Xie 1998; Kirkpatrick et al. 1998; Ren et al. 2000]). The almost exclusive association of subadult males with AMUs indicates male-biased dispersal [Liu et al. 2007; Sicotte and Macintosh 2004]. Judging from low population densities in a fragmented habitat, the bisexual band the bachelor males go after is assumed to be the natal band of most if not all AMU members, as found in geladas [Dunbar 1980].

Fission-fusion

Fission-fusion refers to fluctuations in group size and number of units. Based on the time scale, we distinguish between small-scale/short-term (hours) and large-scale/long-term (days, weeks, months) fission-fusion. Small-scale fissioning, i.e. temporarily dividing into 'subbands' and staying at a distance of several 100 meters was documented on several occasions and seems to have been triggered by human disturbance, travel logistics, and spatial distribution of food items (cf. [Kirkpatrick 1995; Kirkpatrick et al. 1998]). Large-scale fissioning remains a poorly documented and poorly understood phenomenon in

Rhinopithecus. There is anecdotal evidence of fission-fusion on a seasonal basis in *R. roxellana* [Schaller et al. 1985] and *R. brelichi* [Bleisch et al. 1993; Yang et al. 2002]. Others documented more erratic patterns of fission-fusion [Kirkpatrick and Gu 1999; Kirkpatrick et al. 1999; Tan et al. 2003; Zhang et al. 2006]. Theoretically one might expect that fission is related to the mating season, i.e. less band cohesion in the breeding season (late summer/ early fall), as suggested by Kirkpatrick [1996]. However, I documented one long term group split in winter which can be viewed as a strategy to increase the efficiency of resource use in times of overall food paucity [Chapter 7 in this thesis]. If this interpretation is correct, it may have been elicited by the increasingly patchy distribution of valued food resources such as winter fruits (cf. [Anderson 1981; White and Abernethy 2008]). Fission-fusion may well have happened more often, but an unequivocal confirmation is difficult.

Social Interactions

Inter-unit

OMUs are usually permanently within view of other neighboring OMUs. As long as units keep a spatial distance from one another, inter-unit relations are rather neutral and indifferent. Overt aggression, however, ensues when inter-unit distance becomes too small ([Kirkpatrick et al. 1998; this study], cf. also [Zhang et al. 2006]). Absence of constant and escalated aggression among OMU holders may be explained with the familiarity hypothesis, which posits that familiarity between the contestants influences encounter intensity [Ydenberg et al. 1988]. So I would expect more familiar opponents to evoke less intense encounters (*sensu* [Wich and Sterck 2007]). Moreover, OMU leaders may well react differently to other OMU leaders and non-reproductive bachelors, consistent with the threat hypothesis, which posits that the potential threat of the opponent explains variation in the intensity of the encounter [Getty 1987]. A group of western gorillas at Lossi normally responded to lone males by fleeing or displaying, whereas it was frequently tolerant and even indifferent in its meetings with other groups [Bermejo 2004]. AMU males are expected to pose a larger threat and show a higher propensity for takeover attempts and possibly infanticidal attacks (cf. [Steenbeek 2000; Xiang and Grueter 2007]). We are far from an understanding of intermale relations in *R. bieti*, and disentangling the clear nature and context of intermale aggression is challenging given low visibility and extremely large groupings.

The higher rate of male aggression during fall may be related to mating season [Kirkpatrick et al. 1998] or agonistic incursions by bachelors [Cords 1988; Jack and Pavelka 1997; Laws and Vonder Haar Laws 1984] or simply a result of contesting for access to the most valued food item, fruits. Indeed, in this study, there was a positive correlation between the frequency of male aggression and monthly availability of fruit. I also had the impression that large, potentially dominant OMUs monopolized fruiting trees, implying that there is a dominance rank order among OMUs, as has been reported for *R. roxellana* [Zhang et al. 2008b]. I found partial support for the hypothesis that male aggression is elevated when AMUs are present. 'Conception season' did not have an influence on frequencies of male aggression.

While social interactions seem to be confined to within the OMU ([Kirkpatrick et al. 1998; this study], cf. also [Zhang et al. 2006]), sexual interactions may well occur beyond the OMU boundary. *Rhinopithecus bieti* males seem to have much larger testes than other species that show a single male mating system, implying that the breeding system has a promiscuous or (polygynandrous) component [Grüter and Zinner 2004]. I was unable to detect extra-unit matings due to lack of individual recognition, but precisely such have been recorded in a semiprovisioned group of the closely related *R. roxellana* [Zhao et al. 2005]. On the other hand, the low copulaiton rates documented in this study show that the males have more or less a reproductive monopoly in their OMUs.

Intra-unit

Asian colobines are renowned for their low levels of social interaction [Newton and Dunbar 1994; Yeager and Kool 2000]. As measured by grooming, Asian colobines are an unsocial group. Some species, such as *Trachypithecus johnii*, *Presbytis rubicunda*, *P. siamensis* and *P. potenziani* are characterized by an almost total lack of social grooming [Bennett 1983; Davies 1984; Poirier 1970; Sangchantr 2004] (Fig. 3.8). *Rhinopithecus bieti* are relatively social, however, with grooming occupying about 7.3% of the time. This compares well to the 6.1% grooming reported by [Kirkpatrick et al. 1998].

Data on spatial relations and directionality and frequency of grooming allowed me to make preliminary inferences about social affinities and the mechanism that hold the OMUs in this species together. This was done under the following assumptions: 1) Grooming frequency among particular age/sex classes is a good predictor of social bond-formation [Dunbar 1991]. 2) Closeness to a neighbor is an indicator of positive affiliation [White and Chapman 1994]. This latter assumption seems realistic since proximity should signify the

opportunity for positive interactions and the willingness to tolerate some negative effects of proximity, such as increased feeding competition (*ibid*.) or disease transmission.

In Asian colobines in general, social grooming is primarily a female matter [Kirkpatrick 2007]. My data confirm for *R. bieti* that females spent much time grooming socially, which suggests relatively strong inter-female social relationships [Kirkpatrick et al. 1998]. However, consistent with Kirkpatrick et al. [1998], I have found that males also participate in grooming. The amount of grooming activity by males implies that *R. bieti* males are relatively social and affiliative with females when compared with males of other colobines (e.g. [Bennett 1983; Boonratana 1993; Fuentes 1994; Megantara 1989]). Grooming is often viewed as the "cement that maintains social relationships" [Dunbar 1991], and the cohesion produced by male participation in grooming may help to maintain OMU integrity in the midst of a crowded neighborhood with many other units (both bachelor and reproductive) in close proximity. In Chapter 1 in this thesis, it has been shown that Asian colobine social organization (modular vs. non-modular) did not have an effect upon grooming frequency. According to the cross-species analysis on Asian colobines presented in the present chapter, the best predictor of grooming frequency was not group size, but substrate use, implying that the hygienic function of allogroming may become important when terrestrialism is high.

Male social disintegration as typically reported for Asian colobines is also manifested in greater spatial distances between males and other members of the unit [Davies 1984; Kirkpatrick 2007; van Schaik and Hörstermann 1994]. Contrary to this paradigm and in keeping with Kirkpatrick et al. [1998], *R. bieti* males seem to be highly integrated into the social network of an OMU. While controlling for the proportional representation of age-sex classes in the population, I found that females kept close contact primarily with males and males avoided other males almost totally and primarily sought contact with females. The relatively strong social incorporation of *R. bieti* males living in a modular system may be related to the need of male protection against rivals from the loosely associated bachelor groups and other harems. The typically high levels of association in modular societies have the potential to generate conflicts; we would thus expect conciliatory frequencies to be very high since reconciliation is a strategy to preserve social relationships and reinforce unit cohesion, all of which could be jeopardized by conflicts [de Waal 1993; Kummer 1978]. Indeed conciliatory tendencies are high in both captive and wild *Rhinopithecus* (*R. bieti*: 55% [Grüter 2004b]; *R. roxellana* 43% [Ren et al. 1991], >40% [Tan et al. 2008], but also in one species of Asian colobines living in single OMUs (*Trachypithecus obscures*: 46% [Arnold

and Barton 2001]). Another means by which unit cohesion can be maintained is uttering contact calls [Kirkpatrick 1996; Li et al. 1982; Ren et al. 2000]. When traveling in such busy social environs, non-stop vocalizing was common (Grueter, pers. obs.).

Primate social systems have conventionally been divided into male-bonded and female-bonded societies. Most colobine societies resemble the female-bonded pattern although female relationships may be subtle and infrequent as compared to many cercopithecines [Newton and Dunbar 1994]. Recent evidence has gradually refuted the existence of pure male-bonded societies in primates by demonstrating that intrasexual relations are less strictly sex-biased. As an example, chimpanzees and hamadryas baboons have traditionally been placed near the male-bonded end of the spectrum [Goodall 1986; Kummer 1968], but more recent research have shown that females (at least in some populations) do frequently associate with one another and participate in sociopositive interactions [Lehmann and Boesch 2008; Swedell 2002a]. As indicated by grooming relationships and spatial association in *R. bieti*, it seems that the OMUs are held together neither through strong female bonds (as in geladas, [Dunbar 1983]) nor through aggressive male herding (as in hamadryas baboons, [Kummer 1990]), but through bisexual ties: males sustain the allegiance of females through frequent socializing and females have tight bonds with other females. Male policing of female conflicts without the use of overt aggression, as has been observed in captive groups ([Grüter 2004b], see also [Ren et al. 1991]), may stabilize unit cohesion. Males and females have also been observed to cooperatively engage in inter-unit aggressive interactions, both in captive *R. bieti* [Grüter 2003] and semi-wild *R. roxellana* [Zhang et al. 2008b]. In *R. roxellana*, females have also been observed attacking and chasing off their leader male [Ren et al. 2000; Zhang et al. 2006], which is an indication for cohesion among them.

The currently available body of work does not allow me to draw a conclusion about the emigration pattern and OMU foundation in this species, but given that most or all subadult males are associated with bachelor units, male biased dispersal is likely. However, it has also been demonstrated that females undertake both small and large-scale dispersal in *R. roxellana* [Zhang et al. 2008a; Zhang et al. 2006], so limited female dispersal is also possible in *R. bieti*. Female dispersal would be facilitated by the familiarity with and closeness of other units in modular societies [Zhang et al. 2008a]. The temporal fluctuation in unit membership as a result of emigration and immigration can only be assessed via a long-term study following a focal unit, something that is practically enormously challenging under wild conditions.

According to the socio-ecological models [Isbell 1991; Sterck et al. 1997; van Schaik 1989; Wrangham 1980], many aspects of female social behavior depend on the distribution and defendability of food resources. We do not have data on within-unit dominance relationships among *R. bieti* females, but it appears that they exhibit a relaxed and egalitarian system. This egalitarianism is likely the result of diminished *within-unit* feeding competition [Newton and Dunbar 1994; Struhsaker and Leland 1987; Yeager and Kirkpatrick 1998], as patches usually seem to provide sufficient resources for a single *R. bieti* unit [Chapter 8 in this thesis]. To what extent *between-unit* competition (*ibid*.) has an influence on female coalitionary relationships remains uninvestigated. The fact that they feed on both widely dispersed foods (lichen) with low usurpability and clumped foods (fruits, sprouts) with monopolization potential [Zhang et al. 2008b; Chapter 8 in this thesis] makes such an assessment complicated.

Possible Reasons for Band Formation

With regard to socioecological determinants, I have shown in a cross-taxa analysis that ecological factors are unlikely to fully account for the nested nature of the *Rhinopithecus* social system (Chapter 1 in this thesis). In the following, I concentrate on *R. bieti* and briefly discuss some possible explanations for band formation in this species.

Species foraging on resources with a uniform frequency of patch sizes and high density of patches should have larger group sizes [Fimbel et al. 2001; Rodman 1988]. That *R. bieti* at Samage can live in such an unusually large group may be facilitated by the abundance of their staple food [Kirkpatrick et al. 1998; Chapter 7 in this thesis] and possibly lower levels of parasitism in highland areas ([Freeland 1976], but see [Appleton et al. 1986]). However, such a large group confers costs of increased feeding competition [Chapter 8 in this thesis], particularly with regard to spatially clumped and temporally restricted food items. The fact that fission is uncommon leads us to the question of what determinants might stimulate the monkeys to semipermanently congregate in bands.

Predation has long been considered as a major selective force favoring group living in primates [Alexander 1974]. However, predation is nowadays a relatively minor threat to *R. bieti*. Within the range of *R. bieti*, avian raptors prey on infants and small juveniles [Cui 2003b], but they are unable to take adults (cf. [van Schaik and Hörstermann 1994]). Leopards are nearly or fully extinct at Samage, but dholes are still present and domestic dogs are regularly encountered along with shepherds, but no cases of predation are known to me. The

large body size of most *R. bieti* (with males potentially weighing more than 30 kg [Jablonski and Pan 1995] or even up to 50 kg [Ren et al. 2004]) makes them partially or fully resistant to predation (e.g. [Kirkpatrick et al. 1998]). When undisturbed by humans, band members of all age-sex classes occasionally spend a considerable amount of time resting on the ground, indicating a relaxed attitude with regard to ground-dwelling enemies. Predation threat in the past may have been higher as a result of a more intact mammal community and human hunting (likely assisted by dogs), and band formation may have been a strategy to reduce the chance of being preyed upon via vigilance, defense, confusion and dilution. Unfortunately, we lack an understanding of the animals' capacity to adjust group cohesion in relation to changes in predatory threat.

The *localized resource hypothesis* conjectures that highly localized essential or ephemeral resources such as water sites, shelters or food attract several OMUs or force OMUs to congregate at such places. Such resources may be only seasonally available or consistently rare within the habitat. If localized resources were indeed of explanatory value, we would expect the units to assemble only temporally when these resources are available or in spatially restricted places, i.e. fission-fusion should be common. Given that the modular construction is a persistent feature of the *R. bieti* society, localized resources do not seem to have an effect upon band formation. Furthermore, sleeping trees are not limited at Samage [Li et al. 2007] and thus do not provide an explanation for aggregative grouping. Localized resources may, however, be an ecological basis that has initially brought independent social units into proximity and favored a nested grouping pattern. Seasonally fluctuating availability of (food) resources and the heterogeneous vegetation distribution (e.g. Chapter 4 in this thesis) may provoke social units to forage in that part of the habitat where resources are obtainable. This in turn may lead to overlap of home ranges which I regard to be a necessary basis for bringing initially separate OMUs into closer proximity. However, this is just a prerequisite and not a satisfactory explanation for the maintenance of modularity in *R. bieti*.

The *resource dispersion hypothesis* is a favorite among researchers of canid societies [Johnson et al. 2002; Macdonald 1983], but rarely invoked as a possible explanation for group formation in primates (but see [Sussman and Garber 2007]). Slightly modified and adjusted for primates, it would suggest that, as long as resources are heterogeneous and patchy (in space and/or time), the home range chosen by a primary individual or basic social that supplies year-round nutritional and energetic needs for a unit, can also sustain subsidiary units at no considerable net cost to the original unit, thus leading to groups *per se* or higher

level social associations such as snub-nosed monkey bands. So a key prediction is that where resources are patchily distributed and temporally ephemeral (as in habitat mosaic of *R. bieti* within which preferred resources occur in clumps and availability vary with season), an increase in group size may not result in a concomitant increase in home range. However a correlative analysis of 6 *R. bieti* populations for which the necessary data were available has shown that home range size is dependent on group size [Chapter 5 in this thesis], so this basic assumption is not fulfilled. However, one has to keep in mind that larger sampling sizes may revise such a relation because the predictive value of a correlation based on 6 sample points may be limited. Moreover, smaller group sizes in more southerly areas may have been the result of severe habitat alteration and hunting. Even so, we have reasons to believe that some other benefit of sociality overwhelms the disadvantage of increased scramble competition and home range expansion [Macdonald and Carr 1989].

Bachelor threat (a form of conspecific threat) may be a shaping force of the nested societies. This hypothesis posits that OMU holders seek each others' proximity and thereby incur a lower possibility of being challenged by potentially infanticidal and usurping bachelor males, either through active collective defense or through the safety in numbers effect [Rubenstein and Hack 2004; Chapter 1 in this thesis]. I regard the explanatory power of this hypothesis as high for various reasons. First, AMUs routinely follow the mixed-sex bands and associate with them (this study). Second, AMUs can be very large (this study). Third, the presence of AMUs seems to be related to elevated aggression levels of band males (this study). Fourth, males have been witnessed committing infanticide [Xiang and Grueter 2007]. Collaborative defense among unit keepers against male rivals, though, has yet to be shown to be actually operating in these societies. Moreover, with a meta-analysis on Asian colobines, it has been demonstrated that where the expected number of bachelors is high, units have high home range overlap, show higher association degree and have a higher tendency to form bands (Chapter 1 in this thesis). Clearly, more fieldwork is needed to substantiate these assertions. Experimental set-ups under semi-freeranging conditions and artificial approaches such as agent-based modeling may be other promising ways to tackle the problem of determinants of the complex multilevel societies of *Rhinopithecus*.

Appendix

Appendix 1: Behavioral patterns of *Rhinopithecus bieti*

Behavior	Definition	‚Sub-behavior‘	Definition	Notes
Rest	Includes instances when a monkey is apparently stationary or sleeping, usually while sitting (or lying down). Eyes may be open or closed.	Huddle	Resting while encompassing another individual with both arms, or being so encompassed by another individual.	Infants are never assigned to the category of huddle; see ‘cling’.
Vigilance	Peering (staring, glancing) intensely and intently in a certain direction or just scanning the surroundings.			When on the ground they sometimes scan bipedally (mostly juveniles).
Move	Includes any locomotor behavior, including walking or running, that results in a monkey changing its spatial position.			
Play		Auto play	Running about. No other individuals are involved. Movements often not goal-oriented.	Also includes infants moving around on body of adult.
		Social play	Running about, jumping with or without chasing one another, and fighting in a playful context.	
Groom		Auto-groom	Inspection of own fur and skin.	
		Allo-groom	Inspection of another animal’s fur and skin or having one’s own fur and skin inspected by another animal.	
Feed	Inspecting, picking food off plants with hand or mouth, manipulate food, put food into the mouth, and chewing. Does not include inactivity during feeding sessions. Obvious search for food is included as well.			
Aggression	Fighting with, chasing, displacing,			

	threatening another individual.	
Display	Rushing through the canopy, with often exaggerated leaps.	Males, subadult and larger juveniles only.
Cling	Ventral clinging to another individual and being taken on one's lap.	Infants and yearlings only.
Miscellaneous	Includes rare activities not belonging to any of the above behavioral categories	

Appendix 2: Criteria used to tell apart the age/sex classes in *Rhinopithecus bieti*

Age/sex class	Traits[1]
Adult male (AM)	Largest individuals of the band (typically >1.5 x size of other individuals). Elongated white hair on flanks obscures ischial callosities, strong contrast of black and white hair, hair on top of head falls forward, tail long and bushy. Ruff. Perineal region with red strip. White testicles contrast with black inner thighs. Rotund.
Adult female (AF)	Large individuals. Body length (BL) ca ½-1/3 M. Short white hair on flanks, ischial callosities visible, contrast of black-grey and white hair weaker than in males, hair on top of head in a 'top-knot', tail gracile (relative to males). Perineal region with red strip. Black nipples contrast with white chest hair. Often with infants. Typically lithe.
Subadult male (SAM)	At least equal in body size to AF but smaller than AM in body size, testicular size, or both. The contrast of hair is clearer and hair is longer than in females. Tails are relatively hirsute compared with the tails of adult females. Scrotum. Neck ruff not yet fully developed. Overall behavior different from females: sometimes engage in (rough) play behaviour. In general, they are excluded from OMUs, and stroll between OMUs, or form all male units.
Juvenile 3 (J3) [2]	Possibly 3 years. Perineal region with red strip. Small testicles in males.
Juvenile 2 (J2) [2]	Medium-sized individuals. Possibly 2 years. Back and limbs light grey. Tail hair short. Play variable.
Yearling (J1) [2]	Small individuals, light grey. Much play. Travel independently. Occasionally carried by mother ventrally. Sexual discrimination impossible.
Infant grey (I_g)	Second-smallest individuals of band. Coat with light grey on the back. Black strip on top of head. Sometimes agile in travel. Less mother-dependent, more and more play.
Infant white (I_w)	Smallest individuals of band. ≤2 mo. Coat bright white. Not agile in travel. Usually mother-dependent, i.e. carried under mother, but sometimes sitting next to the mother or on the substrate.

[1] Modified from Kirkpatrick [1996].

[2] Distinction among different juvenile classes was often not clear-cut, so I lumped all juveniles together for analyses.

CHAPTER 4 - *Rhinopithecus bieti* in the Samage Forest, China: Use of Habitat

With Dayong Li

Introduction

Broadly speaking, temperate forests with relatively low productivity are an atypical environment for non-human primates. Only very few primate species inhabit forests in temperate regions, e.g. the Nepal gray langur (*Semnopithecus schistaceus*) in the Nepal Himalayas [Curtin 1975; Sayers and Norconk 2006] and the Japanese macaque (*Macaca fuscata*) at several localities in Japan (e.g. [Hanya 2004; Izawa and Nishida 1963]). The four species of snub-nosed monkeys are semi-arboreal and large-bodied leaf monkeys with markedly differing habitat requirements: the gray snub-nosed monkey (*Rhinopithecus brelichi*) is connected with subtropical-temperate mixed deciduous and evergreen broadleaf forest [Bleisch et al. 1993; Wu et al. 2004], the Tonkin snub-nosed langur (*R. avunculus*) inhabits tropical-subtropical hilly evergreen broadleaf forest on karst limestone formations [Dong and Boonratana 2006; Le 2003], and the golden snub-nosed monkey (*R. roxellana*) ranges mostly in mixed deciduous broadleaf/conifer forests, with slight inter-population differences in habitat association [Li Y et al. 2002; Tan et al. 2007]).

Rhinopithecus bieti, the black-and-white or Yunnan snub-nosed monkey, which is geographically restricted to the Hengduan Mountains of Northwestern Yunnan and Southeastern Xizang (Tibet), has long been considered to be primarily associated with high-elevation evergreen fir-azalea forests [Kirkpatrick 1996; Li et al. 1982; Zhao et al. 1988]. More recent studies, though, have demonstrated that the habitats used by *R. bieti* are more diverse than previously thought: they also include forests with deciduous and evergreen angiosperm trees [Ding 2003]. It has been suggested that *R. bieti* use their montane and highly seasonal habitat not only relative to these distinct major forest types, but also adjust altitudinal ranging in relation to seasonal food availability, human activities and temperature [Kirkpatrick and Long 1994; Yang 2003], a phenomenon which we refer to as altitudinal migration *sensu lato*. Altitudinal migration *sensu stricto* refers to vertical movement from

low elevation winter range to high elevation summer range, a pattern that has been particularly well studied in cervids [Albon and Langvatn 1992; Robin 1975].

In temperate-living *Rhinopithecus*, the evidence regarding seasonal variation in altitudinal distribution is conflicting. Differential utilization of altitudinal belts among seasons has been noted by some [Cui 2003a; Happel and Cheek 1986; Hu et al. 1980; Li et al. 2000; Liu 1959; Liu et al. 2004; Wu et al. 2004; Yang 2003]. Conversely, other studies did not find any indication that altitudinal ranging occurs on a seasonal basis [Bleisch et al. 1993; Huo 2005; Kirkpatrick and Gu 1999; Kirkpatrick and Long 1994; Kirkpatrick et al. 1998; Ren et al. 2000; Tan et al. 2007]. Similarly inconsistent results were found for Hanuman langurs (*Semnopithecus* spp.). Migration of Hanuman langurs to lower winter grounds has been postulated (but not actually observed) by [Bishop 1977] for *Semnopithecus schistaceus* at Routang and by [Dolhinow 1972] for southern plains gray langurs (*S. dussumieri*) at Nainital, and observed by [Curtin 1975] in *S. schistaceus* at Junbesi (see also [Vogel 1971]. However, other populations, such as *S. schistaceus* at Simla and Melemchi, did not show a descent [Bishop 1979; Sugiyama 1976].

Here, we present data on the vegetation structure of the different land cover types found in the temperate Samage Forest, an uncommon environment for primates. We studied the snub-nosed monkeys' range use in relation to vegetation type and investigate whether there are seasonal disparities in habitat exploitation. Inferences on altitudinal ranging in this species have been made based on small or incomplete sample sizes and/or indirect evidence such as distribution of faecal pellets. We draw on a long-term study to illuminate the phenomenon of altitudinal migration in *R. bieti* and to identify the factors influencing their seasonal shifts in altitude. Considering that *R. bieti* is at the brink of extinction due to a long history of hunting, logging and other forms of encroachment [Long et al. 1994] and this taxon is still poorly known in terms of its ecological adaptations, its habitat requirements need urgent investigation. This is the first detailed study that quantitatively examines habitat association patterns of *R. bieti*.

Methods

Study Site

We carried out the present study in the vicinity of the village of Gehuaqing (27°34'N, 99°17'E), which is located in the Samage Forest in Yunnan's Baimaxueshan (Baima Snow Mountain) National Nature Reserve (Fig. 4.1). The Samage Forest harbors the largest subpopulation of *R. bieti*, a geographically distinct part of the whole population comprising 2-3 groups of roughly 700 individuals (Ding et al., 2003; Grüter 2004a) and representing ca one third of the total remaining population size [Long and Wu 2006]. For more details on the study site and study group, see Chapter 5 in this thesis.

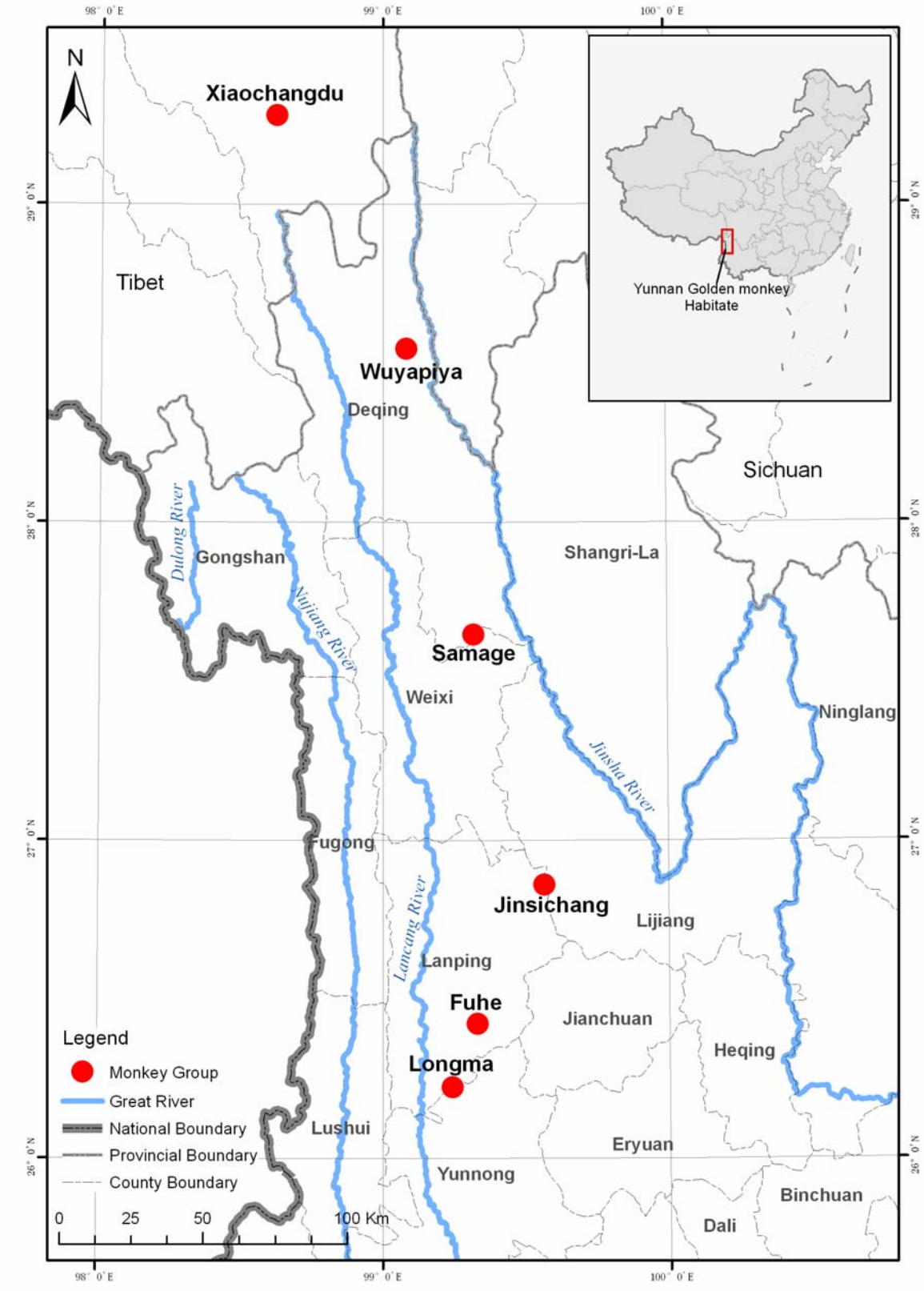


Fig. 4.1. Map of Northwest Yunnan indicating the locations of all investigated groups of *R. bieti* including the one at the Samage Forest that is the focus of this study.

Data Collection

Climatological Monitoring

We recorded daily minimum and maximum temperatures (in °C), precipitation (in mm) and humidity (in %) at the base camp (2448 m) which was equipped with a wireless weather station and a professional weather shelter. We measured the amount of precipitation (usually rain, sometimes melted snow) using a gauge that was connected with the data-logger and transmitted data automatically. Seasons were classified as follows: spring (Mar-May), summer (Jun-Aug), fall (Sept-Nov), and winter (Dec-Feb).

Vegetation Description

We applied stratified random sampling, i.e. we subdivided the forest/habitat into five distinct forest types or strata [Mueller-Dombois and Ellenberg 1974]. The different strata are described fully in the results section of this chapter. We established 67 20 m x 20 m plots in total (area: 26'800 m^2); we laid out 10 plots in pine forest, 12 in evergreen broadleaf forest, 3 in montane sclerophyllous oak forest, 35 in mixed forest and 7 in fir forest. Allocation of plots to the available strata was based on the proportional availability of different vegetation types (stratum weight) within the central part of the study area [Krebs 1999]. We determined the availability of strata through reconnaissance surveys and a GIS (geographic information system) vegetation map. Within each stratum, we placed plots with an objective of sampling at different altitudinal belts (200 m intervals). Within these belts, we laid out plots along existing trails using a random walk procedure, whereby we drew a random number (100-999) and then located a sample plot by taking this number of paces at 500 m intervals.

For each plot, we investigated both abiotic and biotic variables. We assessed aspect of slopes via an electronic compass (E = east = 45°-135°; S = south = 135°-225°; W = west = 225-315°; N = north = 315-360° and 0°-45°). We measured slope inclination in the center of a plot with a clinometer. For slope inclination, we used the following classes: 0°-10°, 10°-20°, 20°-30°, 30°-40°, 40°-50°, 50°-60°. We considered trees to be individuals with girth larger than 40 cm. We recorded the following physical dimensions for all trees in the plots: tree height, crown diameter, bole height and girth. We estimated both tree height and bole height (i.e. height from ground to base of crown) by eye. We paced off crown diameter

directly beneath the tree. To estimate the area of each crown (C), we calculated two diameters taken perpendicularly to each other as:

$$C = (D_1 + D_2 / 4)^2 \pi$$

We computed crown volume using formulae specific to the crown shape. We modelled the crown shape of conifers as a cone:

$$C_V = \pi (D^2 L/12)$$

We modelled the crown shape of broad-leaf trees as an ellipsoid:

$$C_V = 4/3 \ (D/2) \ (L/2) \ (H/2) \ \pi$$

where C_V = crown volume [m^3]; D = crown width; [m]; L = crown depth [m]; H = crown height [m]. We approximated canopy cover in plots using categories: <20%, 20-40%, 40-60%, 60-80%, >80%. We identified tree specimens in plots (n = 1851) *in situ* to species or genus level using reference books (Raven and Wu, 1994-2005; Unknown 1972). If *in situ* identification was not feasible, we collected vouchers which were inspected by staff of the Alpine Botanical Garden in Shangri-La, Yunnan.

Measuring epiphyte biomass is somewhat difficult, and we did not undertake large-scale destructive sampling, i.e. felling of trees. We instead gave each of the marked trees a lichen-load category, i.e. 'None', 'Sparse', 'Light', 'Moderate', or 'Heavy'. We assigned each of these categories a rank from 0 for 'None' to 4 for 'Heavy', to provide a subjective scale to allow comparison among trees. We derived this sampling design from [Kirkpatrick 1996] and [MacLennan 1999].

Group Follows

We were usually able to locate the study group every two or three days based on the animals' signs of presence (scat, food leftovers, prints etc.). On such days, we typically stayed with the group for several hours, and on an average of four days per month also from morning until evening. Observation conditions permitting, we made a record of the group's

position every 30 min. These location records included a reading of the geographical latitude and longitude with a Garmin® eTrex Summit GPS (geographic positioning system) receiver. We also recorded the habitat type in which we encountered the estimated center of mass of the monkey band during a location record. Follows were usually broken off when the group retreated to its sleeping spot or crossed the crest of a hill and moved into another valley. Over the whole 12-month period covered here, we lost track of the study group only on three occasions: in January 2006 for a three-week period (when both field researchers were absent), in February 2006 for a two-weak period (due to heavy snowfalls and the celebration of Chinese New Year), and in June 2006 for another two-weak period (various reasons). We have the impression that all forest types were equally easy or difficult for finding and maintaining visual contact with the monkeys. When some physical barrier prevented us from approaching the group, we could still visually locate the group from bare hilltops or rocky outcrops at a distance of a few hundred meters. Such distance observations were frequently carried out and not only allowed us to have a good overview of the various forest types and see into forest patches that were difficult to reach on foot, but also precluded the possibility that our presence interfered with the group's natural movements.

On a monthly basis, we recorded presence/absence of fruits, flowers and young leaves for 157 food trees and calculated the percentage of trees bearing each of the phenophases every month. For details on phenology monitoring, see Chapter 5 in this thesis.

We conducted field work for this research between September 2005 and November 2006 during which we had contact with the focal group for roughly 800 hours. I used the following data sets for the analyses: total and monthly/seasonal habitat selection ratios: 1 year data, Nov 2005 – Oct 2006 (since sampling effort in Sept/Oct 2006 was much higher compared to Sept/Oct 2005); relations between seasonal/monthly altitudinal ranging and seasonal/monthly climate/human disturbance: 1 year data, Sept 2005 – Aug 2006 (since Fall 2006 data are insufficient due to an early termination of field work in Nov 2006); relation between monthly altitudinal ranging and phenology: 1 year data, Nov 2005 – Oct 2006 (since phenological records of Sept/Oct 2005 are incomplete).

Data Processing

Vegetation cover maps in ArcView 3.3 had been generated by the Institute of Ecology, Yunnan University via a 4-step procedure that can be summarized as follows: 1)

geo-referencing satellite images (Landsat TM), 2) generating polygons by clustering the pixels with similar attributes with a programmed protocol, 3) labeling each type of the polygons based on the image interpretation, and 4) ground-truthing to verify and revise the labels given. Availabilities of resources (vegetation types) can be treated as known, since they were derived from maps which were partitioned into vegetation types. We digitally assessed resource availability, i.e. proportion of each vegetation type within the home range, using GIS (cf. [McClean et al. 1998]). The total home range estimate based on the minimum convex polygon (MCP) method used for this analysis is 50.99 km^2.

Using Manly's terminology, we applied a so called 'study design 1' for measuring resource selection [Manly et al. 2000], i.e. we made all measurements at the population level and individual animals were not recognized. Habitat selection can be regarded as a hierarchical process [Erickson et al. 1998; Johnson 1980]. First-order selection refers to the selection of a geographical area, second-order selection is the habitat composition of the home range, and third-order selection (also called point-range selection) pertains to utilization of habitats within the home range. We assessed habitat use at the third order level, i.e. using the home range *per se* as a definition of availability. We assessed home range during a 14 month study [Chapter 5 in this thesis].

Following [Lopez et al. 2004], we applied habitat-selection ratios as opposed to other inferential statistics because the efficacy of testing point-null hypotheses known to be false *a priori*, e.g. that the monkey band uses available habitat randomly, has been questioned [Anderson et al. 2000; Guthery et al. 2001; Johnson 1999]. We calculated habitat-selection ratios of the group for each habitat type by dividing observed use by availability [Lopez et al. 2004; Manly et al. 2000]. We determined observed use by vegetation type from group follows and associated location records taken at half-hour intervals. The selection ratio for a given habitat type is the ratio of the percentage used to the percentage available [Manly et al. 2000]. Ratios close to one indicate no selectivity. Values less than one indicate selection against that vegetation type while larger values indicate selection for the vegetation type. We determined expected availability by multiplying total location records by the proportion of a given vegetation type/stratum in the monkeys' home range. We then calculated a selection ratio (S) as

$$S = ([U + 0.001]/[A + 0.001])$$

where U = observed use and A = expected use (availability). To avoid zero in the numerator or denominator, we added 0.001 to both use and availability [Bingham and Brennan 2004; Lopez et al. 2004]).

We calculated the Shannon-Weaver index of species diversity (H') to evaluate differences in tree biodiversity among habitat types. The formula is:

$$H' = -\sum p_i \ln p_i$$

where p*i* is the proportion of individuals of the *i*th plant species. SPSS 12.0 was the main software used for statistical data analysis. Tests for significance were two-tailed.

Results

Climate

The study area is characterized by marked seasonality in precipitation and temperature. Winters are generally dry and cold, summers are wet and warm. The wet season is controlled by the southwest monsoon. In winter, a polar front ensures cold and dry conditions with often very strong N-NW winds behind it (cf. [Walker 1986]). 78 % of the rain fell between the months of April and September 2006, the wet season. Annual rainfall was 921 mm. Number of days with precipitation was 140. The highest monthly rainfall was 211 mm in July 2006, the lowest 0 mm in January 2006 (Fig. 4.2). There was a prolonged dry season from November 2005 to February 2006 with minimal precipitation. We recorded the highest humidity (90%) in May 2006 and the lowest (11%) in December 2005 and February 2006. Most snowfalls occurred in February 2006 during which snow accumulated up to 80 cm in depth at an elevation of 3100 m. Higher areas were temporarily off limits due to even greater snow depth.

Mean annual temperature was 14.5°C. Temperatures fell between two extremes of -3.6°C in December and 35.4°C in July. The month with the highest average temperature was July (21.5°C), the month with the lowest average temperature was December (8.3°C) (Fig. 4.2). There were considerable day-night fluctuations in temperature, especially in winter. Greatest daily temperature range was 24.4°C in February, greatest daily humidity range was 65% in November. Since temperature decreases with elevation, the temperature within the

core area of the band's home range at ca 3200 m was approximately 4°C lower than at base camp.

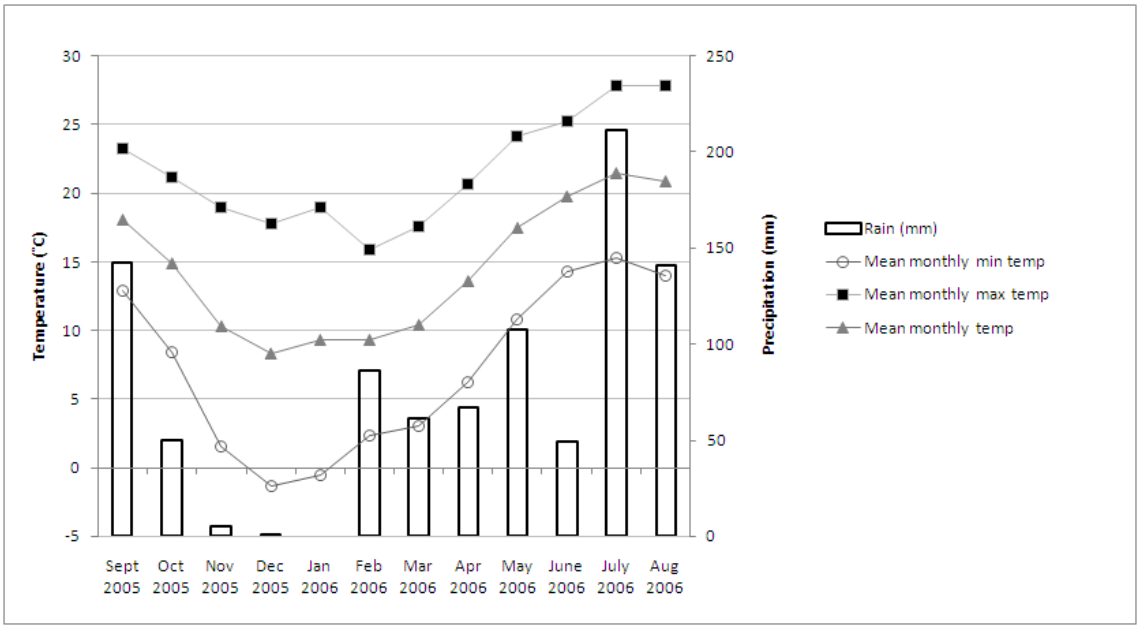


Fig. 4.2. Mean monthly temperature, mean monthly minimum and maximum temperature as well as monthly precipitation at Gehuaqing (2448 m), Samage Forest, in 2005/2006. Precipitation in February was mainly in the form of snow. Data from three days in September are deficient.

Vegetation Composition

We explicitly defined six major vegetation types based on dominant tree taxa, vegetation physiognomy and ratio of gymnosperms to angiosperms (Fig. 4.3): (i) warm-temperate, monodominant and largely secondary *pine forest* on lower south- and west-facing slopes, (ii) subtropical, mesophytic *evergreen broadleaf forest* along valleys, (ii) montane, monodominant, evergreen sclerophyllous *oak forest* on upper (south and west) slopes and along ridges, (iv) polydominant *mixed deciduous broadleaf/conifer forest* on middle and upper slopes (includes stands of bamboo (*Fargesia* spp.)), (v) monodominant cool temperate *fir forest* (dark conifer forest) mainly on ridge-tops (includes selectively logged forest with dense underbush), (vi) *open areas*, i.e. alpine herbfields, mountain shrublands, summer grazing land, grassy meadows, scree and agricultural land. Various azaleas (*Rhododendron* spp.) are widespread in all vegetation communities. Altitude and topography are strongly related to vegetation type and are major factors in differentiating the various habitat forms across the Samage Forest. Additional data on the different strata are given in Tab. 4.1.

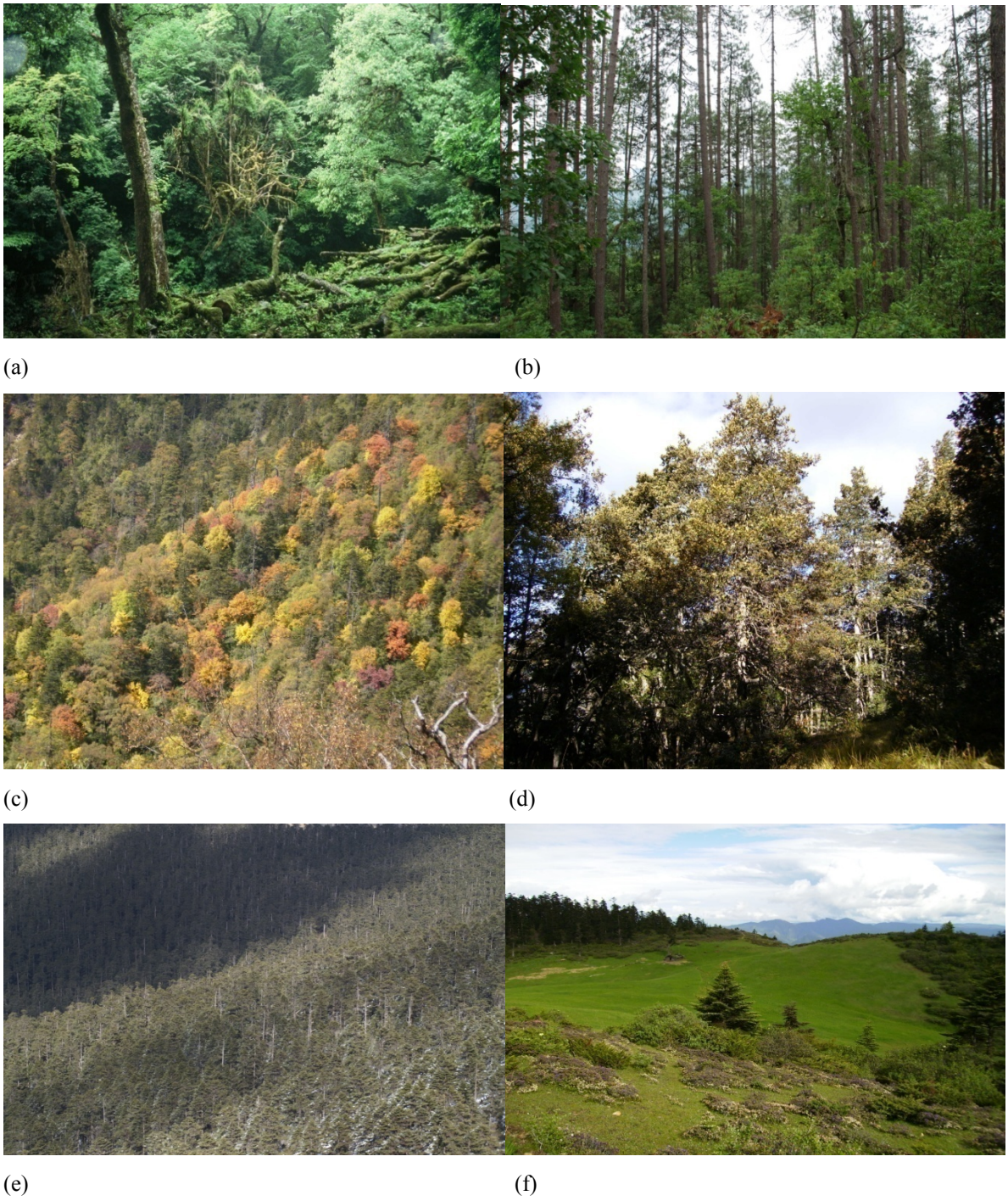


Fig. 4.3. The different vegetation communities in the Samage Forest, Baimaxueshan Nature Reserve, China. (a) Subtropical, mesophytic evergreen broadleaf forest, (b) pine forest, (c) mixed deciduous broadleaf/conifer forest, (d) evergreen sclerophyllous oak forest, (e) cool temperate fir forest open, (f) open areas, i.e. alpine meadows. All photos © C. C. Grueter.

Tab. 4.1. Distribution, composition and structure of different forest types in the Samage Forest, Baimaxueshan Nature Reserve. Means (± standard deviation) are given.

Variables	Mixed deciduous broadleaf/conifer forest (*n* = 969)	Pine forest (*n* = 325)	Evergreen broadleaf forest (*n* = 249)	Cool temperate fir forest (*n* = 241)	Montane sclerophyllous oak forest (*n* = 114)
Altitude [m]	2900-3600	2500-3100	2500-3000	3500-4000	3200-3500
Main canopy species	Various[a]	*Pinus yunnanensis*	*Cyclobalanopsis* spp.	*Abies georgei*	*Quercus pannosa*
Density of trees [ha^{-1}]	697.8 (248.1)	812.5 (239.0)	518.8 (146.6)	860.7 (190.3)	950.0 (413.1)
No. fallen log	3.4 (1.9)	3.5 (2.8)	5.3 (3.8)	2.7 (3.0)	2.3 (2.5)
Tree stumps	2.6 (2.9)	1.8 (1.7)	3.4 (2.0)	1.3 (2.2)	0
Canopy cover [%]	56.9 (17.5)	60.0 (10.5)	60.0 (20.0)	67.1 (13.8)	50.0 (0.0)
Shannon-Weaver index (H')	3.42	1.27	2.48	0.46	1.13
No. tree species	58	10	36	4	10
Ratio gymnosp./angiosp.[b]	0.38	2.14	0.12	8.27	0.11

[a] Main overstory species are *Acanthopanax evodiaefolius*, *Sorbus* spp., *Acer* spp., *Betula utilis*., *Salix* spp., *Quercus rehderiana*, *Rhododendron* spp., *Picea likiangensis*, *Tsuga dumosa*.

[b] Number of gymnosperm stems over number of angiosperm stems.

Average canopy cover of all plots combined is 58.4%. Average height of all sampled trees is 16.8 m and average diameter at breast height (DBH) is 28.5 cm. The distinguished forest strata are noticeably different in terms of overall structure and composition as well as architectural properties of trees (Tab. 4.2). All tree parameters listed in Tab. 4.2 vary significantly among the different vegetation types (DBH: $F_{4,1893} = 14.736$, $p = < .001$; bole height: $F_{4,1893} = 19.562$, $p = < .001$; tree height: $F_{4,1893} = 19.357$, $p = < .001$; lichen load: $F_{4,1893} = 199.771$, $p = < .001$; crown area: $F_{4,1893} = 31.846$, $p = < .001$; crown volume: $F_{4,1893} = 40.211$, $p = < .001$). We found that DBH is largest in evergreen broadleaf forest and smallest in pine forest. Small DBH in pine forest may be due to the fact that this forest contains a sizeable amount of secondary vegetation including young trees. Both bole and tree height are largest in cool temperate fir forest and smallest in mixed forest. Interestingly, the two monodominant gymnosperm strata pine and fir forest are structurally very similar: DBH, bole height and tree height are almost identical. Trees within the evergreen broadleaf forest stratum have the largest crown area and volume.

Tab. 4.2. Variables of measured trees in different forest types at the Samage Forest. Means (± standard deviation) are given.

Variables	Mixed deciduous broadleaf/conifer forest (n = 969)	Pine forest (n = 325)	Evergreen broadleaf forest (n = 249)	Cool temperate fir forest (n = 241)	Montane sclerophyllous oak forest (n = 114)
DBH[a] [cm]	29.3 (19.5)	24.5 (11.6)	34.9 (25.5)	26.0 (11.8)	24.8 (9.4)
Bole height [m]	10.4 (6.0)	12.5 (6.2)	10.7 (5.2)	12.5 (5.5)	12.7 (4.6)
Tree height [m]	15.3 (6.6)	18.8 (7.3)	17.7 (7.4)	18.9 (7.4)	17.1 (4.9)
Crown area [m^2]	27.4 (23.1)	25.9 (18.1)	40.8 (37.4)	21.5 (14.8)	15.7 (9.5)
Crown volume [m^3]	99.7 (151.8)	82.4 (97.8)	242.0 (406.0)	58.4 (72.8)	47.5 (43.9)
Lichen load[b]	1.3 (0.9)	1.1 (0.8)	0.5 (0.6)	2.4 (0.5)	2.2 (0.8)

[a] DBH = diameter at breast height.

[b] See text for details.

In mixed forest, broadleaf trees form a rather closed canopy through which the more widely spaced conifers emerge. This is demonstrated by the density of trees per ha in mixed forest. The mean density of broadleaf trees (n = 708) is 505 stems/ha, and mean density of conifers (n = 263) is 187.5 stems/ha. Moreover, broadleaf trees are smaller-statured than conifers in mixed forest. Mean DBH of broadleaf trees is 25.6 cm (±14.5), and mean DBH of conifers is 39.2 cm (±26.7). Mean tree height of broadleaf trees is 13.6 m (±4.8), mean tree height of conifers is 21.0 m (±8.5). These differences are highly significant (DBH: independent-samples t test, T = 10.127, p < .01, df = 969; tree height: T = 17.094, p < .01, df = 969).

Number of stumps can be seen as an indicator of past logging (highest in the low-lying forest and lowest in the higher strata). None of the forest types is primary *sensu stricto* since selective logging has affected all of them. Diversity varies greatly among forest types, with mixed forest being the most species-rich (58 species) and fir forest being the most species-poor (4 species).

Lichen abundance is higher in temperate strata than in the subtropical stratum and increases with elevation. The only subtropical stratum is the low-altitude evergreen oak forest which has only marginal lichen cover (lichen load index 0.5). Lichen cover is highest in high-altitude fir forest (2.4). Medium-altitude mixed forest has moderate lichen cover (1.3).

Overall Preferences for Floristic Strata

Mixed forest was by far the most frequently used vegetation type at Samage, followed by pine forest, sclerophyllous oak forest and evergreen broadleaf forest. Fir forest was the least frequently used forest type (excluding open areas) (Tab. 4.3). Clearcuts were avoided. We only very rarely encountered the band in severely degraded/altered forest. In our evaluation of habitat-selection ratios, we found that mixed forest was preferred (S = 3.19) whereas all other vegetation types were avoided (Tab. 4.3).

Tab. 4.3. Percentage of each vegetation type at the Samage Forest found within Minimum Convex Polygon-based home range of the Gehuaqing group of *R. bieti* and observed number of location records per stratum in relation to availability. Open areas make up 22.5 % of the area, but were never used and were thus excluded from the analyses. N = 1206 location records.

Vegetation type	Percentage	Expected no. of location records[a]	Observed no. of location records per stratum	Selection ratio	Preference, non-selection or avoidance
Pine forest	16.0	193.0	118	0.611	Avoided
Evergreen broadleaf forest	10.7	129.0	31	0.240	Avoided
Fir forest	37.8	455.9	22	0.048	Avoided
Mixed forest	25.8	311.1	993	3.19	Preferred
Sclerophyllous oak forest	9.7	117.0	42	0.359	Avoided

[a] Based on proportional availability of habitat types.

Habitat Use across Seasons

We found a preference for mixed forest in all seasons and all months (Tab. 4.4) and avoidance or no selection of sclerophyllous oak, evergreen broadleaf, fir, pine forest in all seasons/months. There was a single exception: in September, pine forest was preferred (S = 1.44).

Tab. 4.4 Location records (*n* = 1206) of the *R. bieti* group in the Samage Forest with note on habitat type used in different months and seasons. Meadows excluded

	Mixed forest	Pine forest	Sclerophyllous oak forest	Evergreen broadleaf forest	Fir forest
Nov	69	7	0	0	0
Dec	89	1	0	0	0
Jan	33	0	0	4	0
Feb	28	0	0	0	7
Mar	103	11	0	6	0
Apr	97	19	0	7	0
May	85	0	0	0	0
Jun	51	0	0	0	0
Jul	75	0	0	4	0
Aug	78	3	4	0	15
Sep	206	71	31	0	0
Oct	79	6	7	10	0
Winter	150	1	0	4	7
Spring	285	30	0	13	0
Summer	204	3	4	4	15
Fall	354	84	38	10	0

Vertical Migration along an Altitudinal Gradient

Use of elevations varied significantly among seasons (Kruksal-Wallis, $\chi^2 = 194.69$, df = 3, p = < .001). The lowest recorded elevation was 2625 m, the highest one 3793 m. We also found scat at 4014 m. The most frequently used altitudinal belt was 3000-3400 m, and the mean elevation was 3218 m. The range of elevations used was widest in summer and narrowest in winter. The group stayed at higher elevations in summer than in other seasons, and at lower elevations in spring than in other seasons (Tab. 4.5). The onset of winter did not result in use of lower elevations relative to Fall (Mann-Whitney, $U_{238,172} = 18687$, Z = -1.505, p = .132). However, the group descended temporarily in winter as a result of severe snowstorms; e.g. on March 11th 2006, we located the group at 3500 m, and after 32 mm of snow had fallen at base camp in the meantime, we found the group at 3100 m on March 13th. The range of elevations covered was higher in spring/summer (1168 m) and than in Fall/winter (880 m).

Tab. 4.5. Monthly variation in elevational ranging of the Gehuaqing band of *R. bieti* at the Samage Forest in 2005/2006.

Month	No. location records	Mean elevation [m]	SD[a]	Minimum elevation [m]	Maximum elevation [m]	Elevational range[b]
Jan	40	3112	98	2951	3225	274
Feb	42	3300	199	3100	3747	647
Mar	120	3199	154	2748	3600	852
Apr	124	3060	187	2625	3375	750
May	89	3168	97	2962	3400	438
Jun	53	3423	126	3088	3604	516
Jul	82	3261	187	2674	3546	872
Aug	103	3361	154	3147	3793	646
Sep	55	3381	182	3032	3756	724
Oct	107	3052	122	2876	3335	459
Nov	76	3280	128	3080	3568	488
Dec	90	3238	87	3023	3400	377
Spring	333	3139	167	2625	3600	975
Summer	238	3341	172	2674	3793	1119
Fall	238	3201	197	2876	3756	880
Winter	172	3224	142	2951	3747	796

[a] Standard deviation.

[b] Highest elevation minus lowest elevation in any month.

Data on phenology are presented in Chapter 5 in this thesis. Monthly mean altitude was not correlated with availability of young leaves (r_s = .055, p = .866, *n* = 12 months). This relation is obscured because the time of emergence of sprouts depends on elevation, i.e. leaves appear to mature earlier at lower elevations. However, monthly mean altitude was highly positively correlated with availability of fruits (r_s = .729, p = .007, *n* = 12 mo; Fig. 4.4). In months with high fruit availability, the band stayed at mid-altitudes where favored fruits such as *Acanthopanax evodiaefolius* (Araliaceae), *Sorbus* spp. (Rosaceae) and *Cornus macrophylla* (Cornaceae) are most common (Chapter 8 in this thesis) (Fig. 4.5).

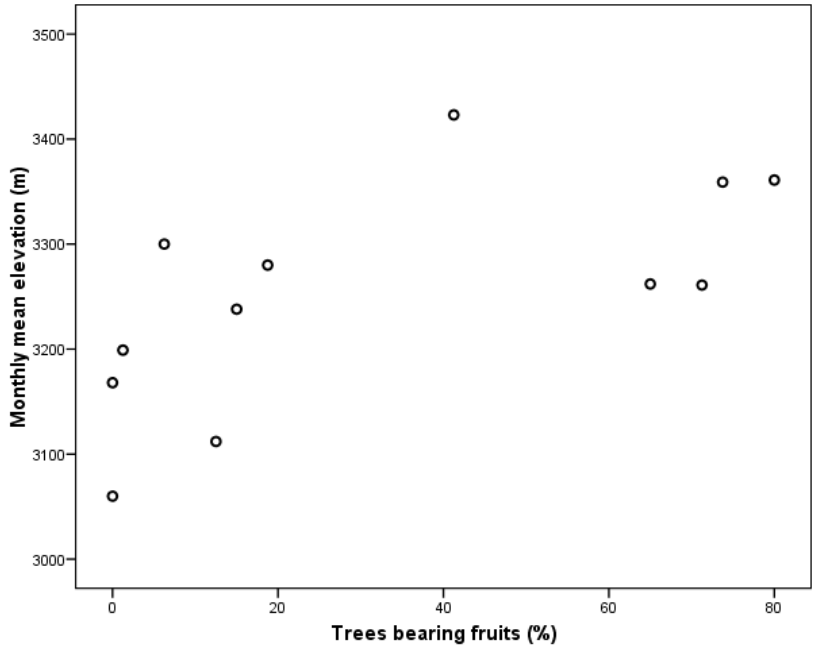


Fig. 4.4. Correlation between monthly mean elevation of the *R. bieti* band at Samage and monthly fruit availability at the Samage Forest.

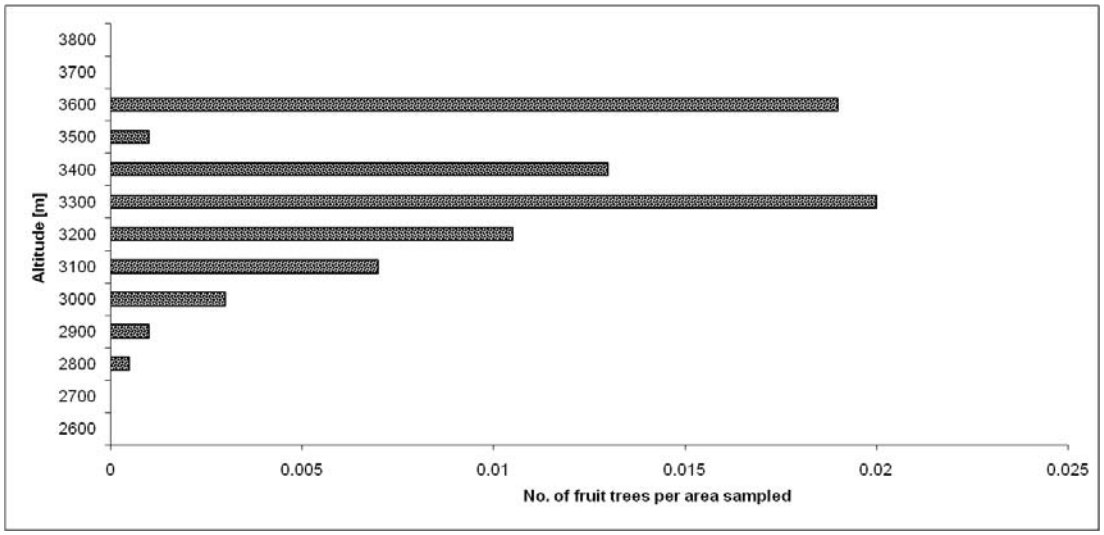


Fig. 4.5. Abundance of major fruit trees (*Sorbus* spp., *Cornus macrophylla*, *Acanthopanax evodiaefolius*) among different altitudinal zones at the Samage Forest. The main fruit trees comprise 138 trees out of 1851 marked trees in vegetation plots. In order to take into account different sampling effort at each elevation, we calculated the number of fruit trees per area sampled. The number of fruit trees (FT) and the size of the area sampled at each elevation is: 2600 m, 0.2 ha, 0 FT; 2700 m, 0.2 ha, 0 FT; 2800 m, 0.2 ha, 1 FT; 2900 m, 0.2 ha, 2 FT; 3000 m, 0.44 ha, 14 FT; 3100 m, 0.28 ha, 20 FT; 3200 m, 0.4 ha, 42 FT; 3300 m, 0.08 ha, 16 FT; 3400 m, 0.2 ha, 26 FT; 3500 m, 0.16 ha, 2 FT; 3600 m, 0.08 ha, 15 FT; 3700 m, 0.2 ha, 0 FT; 3800 m, 0.04 ha, 0 FT.

There is neither a significant correlation between monthly rainfall and monthly mean altitude used (r_s = .294, p = .354, *n* = 12 mo) nor between monthly temperature and monthly mean altitude (r_s = .350, p = .264). Nevertheless, summer had the highest temperature and rainfall at base camp, and the group stayed at the highest elevations where temperature and precipitation were lower. It is possible that human activities did affect the seasonal altitude of the band as well: summer had the largest number of people in the forest, and the band stayed at the highest elevations.

Discussion

Climate and Vegetation at Samage and Other Localities

Striking seasonal variation in ambient temperatures typifies all localities where *R. bieti* has been studied (Tab. 4.6). The average ambient temperature at Gehuaqing/Samage is higher compared to the other sites; this divergence, however, can partly be attributed to the fact that we recorded the climate data about 700 m below the most frequented elevation of the study group. More northern areas, i.e. Wuyapiya and Xiaochangdu, tend to be colder than more southern areas due to higher elevation.

Tab. 4.6. Climate data compared among localities where *R. bieti* has been studied.

Site	Altitude[a] [m]	Highest temperature [°C]	Month highest temperature [°C]	Lowest temperature [°C]	Month lowest temperature [°C]	Mean annual temperature [°C]	Annual precipitation [mm]	Citation
Wuyapiya	4250	16	Jun (5.7)	-13	Feb (-4.9)	0.9	936	[Kirkpatrick 1996; Kirkpatrick et al. 1998]
Xiaochangdu	3800	26.9	Aug (12.5)	-15.4	Jan (-3.6)	4.7	740	[Xiang 2005]
Longma			Aug (14.3)		Jan (1.9)	8.8	1501	[Huo 2005]
Xiangguqing/ Tacheng	2800		Jun (14.9)		Jan (0)	7.5		[Ding and Zhao 2004]
Fuhe	3100	28.1	Jun (14.8)	-9.8	Jan (-0.5)			[Liu and Zhao 2004]
Jinsichang	3280	20	Aug (12.7)	-13	Jan (-3.8)	5.8	1624	Ren B, unpubl.; Yang 2000
Samage/ Gehuaqing	2448	35.4	Jul (21.5)	-3.6	Dec (8.3)	14.5	921	This study

[a] Altitude at which climate data were collected.

George Fir *Abies georgei* typically grows at the highest elevations at all study sites (Table 4.7). Stands of montane sclerophyllous oak are also major components of most sites. Samage appears to be the only locality where subtropical mesophytic evergreen broadleaf forest occurs (but see Huo et al., unpublished). At other sites, e.g. Wuyapiya, low-lying valleys have a completely different vegetation community, i.e. sparse dry scrub [MacLennan 1999] and chaparral [Kirkpatrick 1996].

Tab. 4.7. Availability of vegetation types at other sites where *R. bieti* have been studied[a].

Vegetation types	Fuhe	Xiaochangdu	Longma	Jinsichang	Samage	Wuyapiya/ Nanren
Montane conifer forest	*Abies* sp., *Tsuga* sp., *Larix* sp. 3100-3400 m	Primary and secondary forest with *Picea likiangensis, Abies squamata* 3000-4200 m	*Abies georgei*	Primary forest with *Abies georgei*, *Larix* sp., *Picea likiangensis Rhododendron* sp., *Fargesia* sp. 3300-3900 m	*Abies georgei*, *Rhododendron* spp. 3500-4000 m	*Abies georgei*, *Rhododendron* spp., *Larix* sp. ca 3800-4400 m
Deciduous broadleaf forest	*Sorbus* sp., *Acanthopanax evodiaefolus*, *Fargesia* sp., *Betula* sp. 2700-3100 m	*Betula* sp., *Populus* sp. > 3200 m	(Yes)	*Betula* sp., *Populus* sp., *Fargesia* sp. 3000-3200 m	No	Yes
Mixed broadleaf/conifer forest	*Rhododendron* sp., *Abies* sp., *Tsuga* sp. 2900-3200 m	Not specified	Yes	*Betula* sp., *Populus* sp., *Picea likiangensis*, *Fargesia* sp. 3200-3300 m	*Acanthopanax evodiaefolius*, *Sorbus* spp., *Acer* spp., *Betula* spp., *Quercus rehderiana*, *Picea likiangensis*, *Tsuga dumosa*, *Rhododendron* spp., *Fargesia* spp. 2900-3600 m	*Abies georgei*, *Picea* sp., *Populus* sp., *Quercus* sp., *Rhododendron* sp., *Betula utilis* 3600-3800 m
Pine forest	No	No	*Pinus* spp.	No	*Pinus yunnanensis* 2500-3100 m	*Pinus* spp. < 3600 m
Evergreen sclerophyllous oak forest	No	*Quercus aquifolioides* >3200 m	*Quercus pannosa*	Yes	*Quercus pannosa* 3200-3500 m	*Quercus pannosa* Mainly 3600-3800 m
Bamboo	*Fargesia* sp., *Rhododendron* sp.	No	Yes	*Fargesia* sp. 2900-3900 m	*Fargesia* spp.[c]	No
Open areas	Not specified	*Sabina* and *Rhododendron* shrubs above treeline	Grasslands, shrubs	No	Alpine herbfields, mountain shrublands (e.g. *Rhododendron*), summer grazing land, grassy meadows, scree, agricultural land	Alpine meadows, heath, scree, *Rhododendron* thickets >4200 m; Chaparral and barren rock <3400 m
Subtropical evergreen	No	No	*Quercus acutissima*,	No	*Cyclobalanopsis* sp. 2500-3000 m	No

broadleaf forest		*Lithocarpus dealbatus*
Other	Larch forest; *Larix griffithiana*, *Rhododendron* spp. 3000-4200 m	Stands of azalea; *Rhododendron* sp.(p.)[b]

[a] We extracted data from the following sources: Samage: [Ding and Zhao 2004; Li et al. 2007; this study]; Wuyapiya/Nanren: [Kirkpatrick 1996; MacLennan 1999; Cui 2003a]; Jinsichang: [Yang 2000]; Xiaochangdu: [Xiang 2005; Xiang et al. 2007a]; Longma: table 2 in [Long et al. 1994]; fig. 9 in [Huo 2005]; [Huo et al. unpubl.]; table 5 in [Xiang et al. 2007a]; Fuhe: [Liu and Zhao 2004; Liu et al. 2004].

[b] Whether these are trees or shrubs or both is not specified.

[c] Bamboo is found in the undergrowth of virtually every forest type.

Plant communities vary along an elevational gradient at a single site as well as along a north-south gradient across the whole geographical distribution of *R. bieti.* Specifically, botanical diversity and prevalence of angiosperm trees increases from north to south (cf. [Long et al. 1994]). Increased richness at more southern locations presumably relates to higher amount of precipitation there.

Seasonal and Overall Preferences for Particular Habitats and Comparison with Other Studies

Preferences for particular macro- and microhabitats in primates as a whole have been shown to depend largely on the availability of food (e.g. [Gautier-Hion et al. 1981]; [Hashimoto et al. 1998]) and risk of predation (e.g. [Cowlishaw 1997; Enstam and Isbell 2004]). We have no evidence of predation threat being lower in the frequently used forest types at Samage. The *R. bieti* group at Samage did not use the study area homogenously, but showed a clear preference for mixed forest. Possible reasons for over- and underutilization of particular floristic strata are discussed in the following.

The location records of *mixed forest* make up 82% of all positions. Mixed forest is distributed between 2900 and 3600 m, which corresponds to the most frequently utilized altitudes of *R. bieti* at Samage. We suspect that food resource abundance in this stratum accounts for its preferred use. Mixed forest contains the highest diversity of tree species and the highest variety of food items (Chapter 8 in this thesis). The importance of mixed forest in providing food sources has been previously documented at other sites [Ding and Zhao 2004;

Liu et al. 2004]. Lichen load is intermediate in this stratum, but the temporal appearance of fruits and sprouts makes this stratum nutritionally valuable. Mixed forest is also the forest type where most of the sleeping sites were found [Li et al. 2007].

Pine forest has been regarded as unsuitable habitat [Xiao et al. 2003; Huo et al. unpublished], and use of this stratum has often been seen as aberrant, e.g. induced by human herding. However, our results demonstrate that the Gehuaqing group spontaneously visits pine forest from time to time. [Ding and Zhao 2004] also note that the group at Xiangguqing occasionally spent time in secondary warm-temperate conifer forest, i.e. pine forest. The underlying cause for the preference of pine forest in September remains unclear. However, as a whole, no selection was shown for pine forest in fall and annually. The main canopy species *Pinus yunnanensis* does not offer any food to the snub-nosed monkeys. Seeds of *P. armandii* are an important part of the late fall/winter diet in both *R. bieti* at other sites [Huo et al. Unpublished] and *R. roxellana* [Li 2006], but ingestion of those seeds has not (yet) been witnessed at our site. *Pinus armandii* at Samage is equally associated with mixed forest and pine forest, and occurs at fairly low stem densities in both strata. Pine forest has a moderate lichen density. Pine forest often covers some of the lower ridges, and some of the band's frequently used travel routes leading from one patch of mixed forest to another cross this stratum. It is thus assumed that pine forest acts as a corridor and is visited in transit. Yunnan pine forest also holds an economically precious resource for humans, the highly prized Matsutake mushroom. This forest is thus frequented by mushroom hunters in summer and fall, which may prevent the monkey group from moving into pine forest and obstruct the group's passage to other patches of mixed forest.

Rhinopithecus bieti have often been viewed as inseparable from *cool fir forest* or *dark conifer forest*. However, dark conifer forest is evidently not the preferred habitat type at our study site. Occasional visits to this stratum in winter may be related to obtaining omnipresent beard lichens of the genera *Usnea* and *Bryoria*, which are more abundant in fir forest compared with other strata and form the staple food of the Gehuaqing band [Chapter 7 in this thesis]. Contrary to groups living in the north, the group at Samge is not as strictly dependent on lichens and makes use of a range of alternative non-lichen food items such as fruits, and this may explain why fir forest is uncommonly visited here. Due to the fir forest's location on semi-isolated hilltops at the highest elevations, the band is obliged to traverse through this forest when crossing ridges and thus uses it in a transient fashion. Several investigations at different localities have provided evidence that high-elevation conifer forest is rarely (mostly

in summer) or never used by *R. roxellana* in relation to deciduous broadleaf forest and (to a lesser degree) mixed forest [Hu et al. 1980; Zhang 1995; Li et al. 2000; Tan et al. in 2007]. Similarly, *Macaca fuscata* in the Shiga Heights have been observed to avoid the conifer zone and stay in the broadleaf zone [Wada and Ichiki 1980].

Lush semihumid *evergreen broadleaf forest* is confined to valley bottoms, and it is used often in passage from one mountain slope to another. This forest also contains ample water sources, and group members have been seen drinking from streams there. Furthermore, the season with the highest number of positional records in this stratum is spring. In early spring, shoots emerge first at lower elevations [Ding and Zhao 2004], possibly causing the band to move along this low-lying altitudinal zone which inevitably results in visits of evergreen broadleaf forest. Current anthropogenic activities such as illegal logging may have caused the overall avoidance of this forest type, and it seems that this forest was avoided in the past as well when mass killings of snub-nosed monkeys for food and commercialization took place there in the 1960s/70s (Feng Shunkai, pers. com.).

Feeding on acorns has thus far only rarely been observed at our site, but Xiang et al. [2007a] for instance found that the group at Xiaochangdu visited *sclerophyllous oak forest* for acorns in fall and winter. High lichen availability and seasonal occurrence of acorns may explain why this forest type was particularly often used by the Gehuaqing band in fall.

A probable explanation for the total avoidance of *open areas* includes the absence of tall trees providing cover and the grazing of cattle during the warmer months. At Samage, grasslands hold a few bushes with berries, but are otherwise of minor importance with regard to food sources. Li [2004] also found that groups of *Rhinopithecus roxellana* at Shennongjia did not use grassland. At Zhouzhi, clearcuts and heavily logged forests were only used in transit [Guo 2004].

Seasonal Altitudinal Migration

We found that the Gehuaqing group showed seasonal adjustments in use of altitudes and basically stayed at relatively high elevations in summer, low elevations in spring and moderate elevations in winter and Fall. Our data precisely correspond to Cui [2003a] whose results are based on indirect estimations using distribution of faeces of a monkey group at Baimaxueshan North. Yang [2003] investigated seasonal distribution of faeces of the Jinsichang group along an elevational gradient and found a comparable result: summer > fall

> winter/spring. Liu et al. [2004] lumped two seasons together and found the following pattern for the group at Fuhe: summer/fall > winter/spring. In addition, the West Ridge troop of *Rhinopithecus roxellana* exhibited an analogous pattern of altitudinal ranging: summer > fall > winter/spring [Li et al. 2000]. The results of the latter three studies diverge from ours insofar as they also demonstrated use of lower elevations in winter. Apart from the discrepancy as to the descent in winter, the existing evidence indicates that altitudinal ranging in snub-nosed monkeys may follow a general underlying principle, i.e. it is influenced primarily by diet and only marginally by climate and human encroachment.

As mentioned above and in the introduction, evidence for a descent in winter as a response to cold has been mixed. Yang [2003] for instance found a positive correlation between temperature and elevational distribution of the Jinsichang band whereas others found that the monkeys constantly chose the upper forest sections, even in cold snowy winters [Cui and Zhao 2002; Zhao et al. 1988]. Even though movements to low elevations do not appear to be a general feature of *Rhinopithecus* ecology, short-term descents to lower altitudes as a result of heavy snowstorms have been observed ([Cui 2003a; Kirkpatrick and Long 1994; Li et al. 2000; Shi et al. 1982; Xiang 2005; this study]; see also [Tan 1985]). Our observation that snub-nosed monkeys remained at fairly high elevations when temperatures dropped in winter lets us conclude that they do not fine-tune their altitudinal ranging pattern in a systematic way to *climate* by staying a lower elevations when temperatures drop in winter and staying at higher elevations when temperatures rise in spring. However, inclement *weather* conditions such as heavy snowfalls and snowstorms seem to force them to temporarily move down into the valley with milder temperatures and shallower snow depth.

While winter cold did not affect altitude use, summer heat, on the other hand, may have had an effect. In summer, the band possibly sought refuge at high elevations and thereby escaped the heat at lower elevations. Even though the correlations were not significant, summer had the highest temperature and rainfall at base camp, and the Gehuaqing group stayed at the highest elevations where temperature is ca 5°C lower and amount of rainfall is also less (cf. [Li 1993]). Li et al. [2000] also hypothesized that *Rhinopithecus roxellana* look for cooler high elevation places in summer.

In montane primates, the lower end of their elevational range is often set by human colonization. It is still not entirely clear, however, to what degree human presence and activities inside the habitat impinge upon altitudinal range use in *R. bieti*. MacLennan [1999] states that “there appears to be a strong correlation between seasonality of valley use by the

monkeys and an absence of human activity in that area, with monkeys apparently using sites just before or just after peak human activity." Kirkpatrick et al. [1998], however, concluded that human activity did not appear to influence the mean altitude of the Wuyapia band, living close to herders yet remaining at high altitudes when human activity above 3500 m was minimal. At our site, the evidence is also ambiguous, and no strong effect of human activities on general range use is evident [Chapter 5 in this thesis]. Increased anthropogenic pressure in summer may have brought about a consequent upward movement. Contrary to expectations, when human encroachment as a constraining factor was minimal or absent in winter, the group still used fairly high elevations.

That diet is the driving force behind altitude use is manifested in many ways. Leafing or flush of deciduous trees in spring is assumed to have triggered the use of lower elevations. Immature leaves form a dominant constituent of the snub-nosed monkeys' diet in spring and become available earlier at low elevations compared to high elevations (cf. [Hu et al. 1980; Shi et al. 1982]). The Gehuaqing group covered a wider range of altitudes in spring-summer (when young leaves were available) compared to fall-winter (when young leaves were absent). Moving along an ascending altitudinal gradient during spring-summer ensures fitness gains via a prolonged access to newly emerging foliage of high nutritional quality ([Guo et al. 2004; Tan et al. 2007]; cf. also [Mysterud 1999]).

As evidenced by a highly significant correlation between monthly fruit availability and altitudinal distribution of the band, fruiting had a strong effect on altitude use as well. In fall, when fruit availability was maximal, the study group confined its raging to moderate altitudes where the density of preferred fruits was highest. Even in winter, the band kept foraging at middle altitudes in search of fruits from the preceding fruiting season.

Since climate can be ruled out as a general determinant of altitude use, the study group's occupancy of relatively high altitudes in winter is likely related to higher concentrations of lichens at higher elevations (cf. [Kirkpatrick et al. 1998; Kirkpatrick and Gu 1999]). The relation between food density and altitudinal ranging was further confirmed in a study by Cui [2003a] who found more faeces at altitudinal zones with dense lichen cover. Our study corroborates these findings: lichens as the major winter food occur at higher densities at higher elevations at Samage (Chapter 7 in this thesis). These arguments are fundamentally similar to Sugiyama's [1976] observations of *Semnopithecus schistaceus* remaining at high altitudes in winter due to greater abundance of conifer-based foods. Likewise, Mehlman [1986] observed that Barbary macaques (*Macaca sylvanus*) stayed at

highest altitudes in snowy winter because their main food - fir foliage - is found at high altitudes.

Harvest of bamboo shoots (*Fargesia* spp.), which represent a seasonally important food source [Ding and Zhao 2004], may also have caused the band to seek higher altitudes in summer. Bamboo shoots as a seasonal key resource also influence range use of Grauer's gorillas (*Gorilla beringei graueri*) at Mt. Kahuzi which have been reported to show an annual cycle of migration corresponding to the availability of bamboo shoots [Casimir and Butenandt 1973].

What Constitutes the Natural Habitat of *Rhinopithecus bieti*?

An understanding of a species' extant habitat requirements is incomplete without considering palaeobiogeographic events and the history of anthropogenic habitat alteration. Environmental fluctuations during the Quaternary period are assumed to have influenced the distribution and habitat association of snub-nosed monkeys [Jablonski 1993]. For example, the termination of the glacial periods in the Holocene brought about vegetation changes along an elevational gradient. Fir forest subsequently became restricted to mountain ridges, and this reduction in fir forest reduced the range of *R. bieti*. Anthropogenic forces (population explosion, deforestation, cultivation) in recent and historic times have led to large-scale destruction of suitable habitat at medium elevations and extinction of some populations of *R. bieti*. This is corroborated by the fact that historical records exist from *R. bieti* populations farther south than its current distribution. The historic distribution of Chinese snub-nosed monkeys in general also included lowlands in several provinces and has become gradually confined to the highlands through the combined effects of habitat destruction and hunting [Li B et al. 2002a; Li et al. 2003].

Rhinopithecus bieti was initially considered to be a characteristic species of the high-elevation fir forest ecosystem. Even recent reviews proclaim that *R. bieti* is "definitely associated with fir forest" [Li et al. 2003]. Subsequent studies, though, found that this taxon in fact exhibits a greater diversity and flexibility with regard to habitat affiliation. Similarly, Barbary macaques being found in a number of habitats in the Mediterranean climatic zone of North Africa, were first seen as cedar forest specialists [Taub 1977]. A re-examination of data on distribution and abundance, however, refuted the idea of cedar forests constituting their preferred habitat and instead revealed that their primary occurrence in cedar forest represents

an artifact produced by elimination from other forest types due to historic anthropogenic forest destruction [Fa 1984].

The fact that an array of discrete vegetation types is found within the home range of the more or less free-ranging group of *R. bieti* at Samage provides a good opportunity to investigate habitat association patterns. Our findings that cold temperate fir forest is largely avoided by *R. bieti* provides strong evidence that milder mixed forest may represent their characteristic habitat and that high dependence on fir forest as shown by some groups living in the far north may be at least partly a consequence of past human habitat modification.

Habitat association and altitudinal distribution of most known groups of *R. bieti* are given in Tab. 4.8. Fir forest typifies for the most part the habitat in Tibet and other localities in the north, whereas more mixed forests are found in more southern regions. Mixed forest does occur at localities in the north as well, but may differ from the mixed forest at more southern localities by being less nutritionally valuable and having a different species composition.

Tab. 4.8. Habitat association and altitudinal distribution of groups of *R. bieti*[a].

Site	Lowest elevation [m]	Highest elevation [m]	Mean elevation [m]	Geographical area	Mainly used forest type	Citation
Wuyapiya	3300	4600	4080	North	Fir	[Kirkpatrick et al. 1998]
Nanren	3500	4300	ca 4050	North	Fir	[Cui 2003a]
Xiaochangdu	3500	4250	4031	North	Fir	[Xiang 2005]
Gehuaqing/Samage	2625	4014	3218	Middle	Mixed	This study
Xiangguqing	2700	3700	ca 3200		Mixed	[Ding 2003]
Fuhe	2800	3400	3105	South	Mixed, fir and deciduous broadleaf	[Liu et al. 2004; Liu and Zhao 2004]
Jinsichang	3200	3630	3500	South	Mixed[b]	[Yang 2003; Ren B, unpubl.]
Longma	2700	3600	3024	South	Mixed	[Huo 2005]
Zhina	-	-	-	-	Fir and evergreen oak[c]	[Xiang et al. 2007b]
Milaka	-	-	-	-	Fir and evergreen oak[c]	[Xiang et al. 2007b]
Bamei	-	-	-	-	Cypress	[Zhong et al. 1998]

[a] Elevation data also based on scat findings.

[b] [Yang 2000], however, claims that dark conifer forest constitutes the main type at Jinsichang.

[c] Possibly of the sclerophyllous type.

Implications for Management and Conservation

If animals select habitat and habitat-specific resources disproportionate to their availability, it is commonly concluded that this habitat or resource is of relatively higher quality and enhances fitness, i.e. survival or fecundity. Thus, data on habitat selectivity is often employed to manage supposedly important habitats for the target population. However, frequent use may not be correlated with habitat quality and suitability and fitness [Hobbs and Hanley 1990; Garshelis, 2000; Jones 2001]. Correspondingly, infrequent use may not be indicative of lack of suitability. Garshelis [2000] pointed out that "a habitat may be used infrequently because it serves little value, because its value can be extracted in a short amount of time, because it is not readily available, or because access is constrained by threats (social pressures, competition, predation) or physical barriers". Infrequently used habitats are thus better seen as habitats of relatively little value instead of unsuitable habitats. Sclerophyllous oak forest for example may be used less because it is not readily available at Samage. Even cool temperate fir forest may be used slightly more often if it were not semi-isolated due to man-made barriers, i.e. grazing land. The value of pine forest and evergreen broadleaf forest can be extracted in a short amount of time because they mainly serve as transit habitats (both) and watering-places (evergreen broadleaf forest only).

All forest types at Samage show signs of human alteration, mainly in the form of past and present selective wood extraction for commercial and subsistence purposes. The forest types least affected are sclerophyllous oak and fir forests. The lower areas of the pine forest zone close to the agricultural fields are the main source of firewood and construction material and hence the target of intensive tree cutting. This buffer zone was never used by the snub-nosed monkeys.

Even though Baimaxueshan Nature Reserve was primarily set up to promote protection of the snub-nosed monkeys, the heterogenous habitat with interspersed grazing land implies that large areas of the reserve do not represent monkey habitat. In spite of the fact that *R. bieti* is semi-terrestrial (e.g. [Xiang 2005]) and animals have been witnessed going to open areas on occasion (e.g. [Kirkpatrick 1996]), we have no location records for open areas. Hence clear-cutting is assumed to have a fatal effect by rendering these areas uninhabitable to the monkeys.

The overwhelming preference for mixed forest by *R. bieti* underscores the significance of ensuring protection of this type not only at Samage, but also at other sites where black-and-white snub-nosed monkeys occur and where some type of habitat

manipulation is proposed. Evergreen broadleaf, pine and fir forests do not represent prime snub-nosed monkey habitat, but nevertheless provide vital forest corridors that must be preserved at all costs to maintain connectivity between forest patches.

CHAPTER 5 - Characteristics of Range Use of *Rhinopithecus bieti* in the Samage Forest, China

Introduction

Range use in colobines (Colobinae) and other primates is determined by an assortment of eco-behavioral factors. These include precipitation [McKey and Waterman 1982], temperature [Yang 2003], the quality as well as availability and distribution in time and space of food [Agetsuma and Noma 1995; Barton et al. 1992; Bennett 1986; Clutton-Brock 1975; Curtin 1982; Fleury and Gautier-Hion 1999; Pages et al. 2005; Zhang 1995], group size [Fashing et al. 2007b], sleeping site or resting site location [Davies 1984; Liu et al. 2004; Rasmussen 1979; Zhou et al. 2006; Zinner et al. 2001), proximity of conspecific groups [Fashing 2001a; Struhsaker 1974; Waser 1976], predation pressure [Boinski et al. 2000; Treves 2002], anthropogenic disturbance [Li et al. 1999; Li et al. 2005], polyspecific associations [Holenweg et al. 1996], and day length [Li 2002]. It has long been known that colobines have shorter daily path lengths and smaller home ranges than most other primates [Chapman and Chapman 2000]. The typically small range sizes and short daily travel distances in many colobines may be caused by energetic constraints attributable to their specialized digestive tracts and relatively folivorous diets, and their dependence on uniformly distributed and ubiquitous food resources [Kay and Davies 1994].

Nevertheless, colobines exhibit a tremendous variety of ranging styles: on the one extreme, some populations of guerezas (*Colobus guereza* [Leskes and Acheson 1971; Schenkel and Schenkel-Hulliger 1967]) and purple-faced langurs (*Trachypithecus vetulus*) occupy tiny home ranges and are almost stationary [Hladik 1977], while populations of Angolan colobus (*Colobus angolensis*) in Rwanda (Fashing et al. 2007b), black colobus (*Colobus satanas*) in Gabon [Fleury and Gautier-Hion 1999] and black-and-white snub-nosed monkeys (*Rhinopithecus bieti* [Kirkpatrick et al. 1998]) occupy vast areas, show long-term range expansions and are semi-nomadic in nature.

The question arises as to why some colobines exhibit large home ranges and even are semi-migratory? It is not simply that large range sizes are a feature of those colobines living

in resource-poor environments such as temperate forests, even though this is demonstrated by some species including pale-armed Himalayan langurs (*Semnopithecus schistaceus*) and *R. bieti* [Curtin 1975; Kirkpatrick et al. 1998]. *Colobus angolensis* at Nyungwe and *C. satanas* at the Forêt des Abeilles follow a comparable strategy, but live in more productive tropical habitats, i.e. in montane mixed moist forests and lowland moist forests, respectively [Fashing et al. 2007b; Fleury and Gautier-Hion 1999]. The large ranges in *C. satanas* are assumed to be caused by the irregular fruiting of the Caesalpinaceae, an essential food source [Fleury and Gautier-Hion 1999]. Based on established socioecological theory (e.g. [van Schaik et al. 1983]), we should expect a larger group to occupy a larger home range to satisfy its energy requirements. In Nyungwe, it is probably the very large group sizes of more than 300 that necessitate such wide ranges [Fashing et al. 2007b]. Kirkpatrick et al. [1998] considered lichens to be a critical factor influencing ranging of a *R. bieti* band living in an alpine-temperate and very seasonal forest in North Yunnan, China: they argued that, since lichens replenish only very slowly, monkeys need to forage nomadically to allow lichen-depleted patches to recover to a harvestable level between visits. Furthermore, they hypothesized that the "readily digestible energy in lichens may release *R. bieti* from the short travel distances associated with leaf-eating".

Black-and-white snub-nosed monkeys (a. k. a. golden monkeys) are characterized by behavioral and ecological strategies that differ in many respects from other colobines, the aforementioned large ranges being just one of them. They are found at the upper limit of elevation (as high as 4700 m) and latitude for any nonhuman primate and inhabit subtropical-temperate or purely temperate forests [Long et al. 1994]. Their use of food resources reaches an extreme in some populations that rely almost exclusively on tree lichens [Kirkpatrick 1996]; other populations in more productive environments, however, do have a more diversified diet largely moulded by phenology [Chapter 8 in this thesis]. Moreover, groups of *R. bieti* are invariably large and can contain up to several hundred members [Grüter and Zinner 2004].

Only about 17 groups of *R. bieti* are left in the wild [Long and Wu 2006], and only a few of them are suitable for obtaining an unbiased estimate of their range use. Some groups are restricted to forest islands in a sea of farmland/grazing land [Xiao et al. 2003] and thus are no longer able to exhibit a natural ranging pattern. One group is regularly herded by humans for tourist viewing purposes thus obscuring natural ranging tendencies [Grüter 2004a], and others are so elusive that even a long-term study does not permit more than a handful of

sightings [Yang 2000]. In order to overcome the last problem, other researchers investigated the distribution of faeces as evidence of the snub-nosed monkeys' ranging [Cui 2003a] or used GPS collars to track them [Ren et al. 2004]. In the current study, I directly followed a single band of *R. bieti* for a prolonged period spanning more than one year.

The aims of this study were to characterize the spacing system of *R. bieti* at a locality in the central area of their geographic distribution, verify initial reports of their semi-nomadism, document whether they use their home range in an even manner or exhibit seasonal range compression/expansion, and tackle the question of why home ranges in this species are so extraordinarily large. Since one of the main determinants of their ranging may be the seasonally variable abundance of specific food items, we assessed temporal availability of food by monitoring phenology of food trees on a monthly basis throughout the study period. I also investigated the correlation between ranging and climatological parameters as well as anthropogenic factors that are assumed to interfere with the monkeys' natural range use. Range use is often linked to demography [Chapman and Chapman 2000], and the interrelation between the two is another focus of this study. Specifically, I compared group size and home range size of different groups and checked for effects of scramble competition, as found in several primate taxa (e.g. [Barton et al. 1992]. Environmental variables such as floristic diversity and composition, elevation and climate have been demonstrated to vary substantially across sites within the distribution of *R. bieti* [Long et al. 1994]. I therefore asked whether such differing environmental conditions lead to within-species variation in range sizes. In particular, I tested whether there is a negative relationship between range size and habitat quality or productivity, as found in previous studies of primates in temperate forests [Bishop 1979; Jiang et al. 1991].

Methods

Study Area and Study Subjects

I conducted the present study between September 2005 and November 2006 in the Samage Forest near the town of Tacheng and the village of Gehuaqing in Weixi County of Yunnan Province, PRC (27°34'N, 99°17'E). The Samage Forest forms the southernmost part of Baimaxueshan Nature Reserve. The research area encompasses around 40 km^2 of subtropical to temperate forest interspersed with clearcuts and cattle grazing land and spans an altitudinal

range of 2500-4000 m. The mountains are part of the Hengduan Mountain Range at the Eastern margin of the Tibetan Plateau. Annual rainfall was 921 mm, and mean annual temperature was 14.5°C at 2448 m (800 m below the most frequently used altitude of the study group). Temperature and precipitation vary strikingly with seasons (for details on climate, see chapter 4 in this thesis). Forest cover at the research area is a mosaic of mixed coniferous and deciduous-broadleaf forest, high-elevation fir forest (*Abies georgei*), evergreen oak forests of different kinds (mesophytic lowland *Cyclobalanopsis* spp. and montane xerophytic *Quercus pannosa*) and pine forest (*Pinus yunnanensis*). Topography is made up of precipitous slopes. Parts of the Samage Forest have been selectively logged, and human encroachment in the form of livestock grazing and harvest of non-timber forest products is commonplace. The focal group (Gehuaqing group) is composed of ca 410 members. The group has become fairly well habituated after years of continued surveillance by reserve staff. Another large group (Xiangguqing group) is found ca 10 km to the east of the Gehuaqing group. The only other sympatric primate is the rhesus monkey *Macaca mulatta*.

Data Collection

We located the study group based upon its position during previous observation days and information about the animals' whereabouts gained from field assistants. After establishing visual or auditory contact (vocalizations, sound of breaking branches) with the group, we took a location record of the group's center every 30 min using a GPS receiver (Garmin® eTrex Summit), unless that was made impossible by dense vegetation and deep valleys. Since I usually observed the group from lookout points up to several hundred meters away, I corrected positions for distance to the group using a laser rangefinder (Bushnell ®) and an electronic compass.

The *Rhinopithecus* lifestyle called for a somewhat flexible study design. Instead of undertaking conventional dawn-to-dusk group follows during several consecutive days, we trailed the group whenever conditions were favorable and established contact with the group on an average of 12 days per month (Tab. 5.2). A conventional five-day-per-month sampling regime would have resulted in a drastic underrepresentation of the monthly home ranges because the group covers much larger areas over the course of a whole month. Similarly, it would have been unsuitable for estimating daily travel distance in this species for two

reasons. First, the group sometimes spent time in areas not accessible to researchers, resulting in missing data in that month. Second, *R. bieti* is known to alternate between long-distance movements and concentrated use of relatively small areas. Such uneven ranging may cause strong biases in monthly estimates of daily travel distance if based on only a few days per month.

We were seldom able to make full day follows and obtain accurate data on daily travel distance because continuous tracking of the group is challenging when the animals engage in long-distance travel. They are fast moving, sometimes go out of sight and may wander into areas which are off-limits to researchers. In addition, group spread is often large, and determining the group center is often difficult when following the group. Hence, daily travel distance calculation based on consecutive GPS points are probably not very exact since the portion of the group geo-referenced need not be the group center. Nevertheless, in September 2006, when additional manpower was available, we followed the group continuously for a whole month. September was chosen because it seemed to be a representative month in terms of day range and day to day travel (based on our data from September 2005 and additional data on daily travel distance collected in other seasons after the termination of this study).

Data Analysis

Range Use

For the calculation of the total home range size, we recorded the grid cells entered by the monkey group. We chose 250 x 250 m grid cells because we found the usual spread of the band to be around 200 m. We calculated range size as such:

$$(\text{number of cells entered}) \times (0.0625\ \text{km}^2) / \cos(40°)$$

Cos(40°) stands for the approximate average angle of slope obtained from a field survey at Samage (cf. [Tan et al. 2007]). The total home range was based both on sightings of the group itself and signs of its presence such as fresh scat. We also took coordinates of positions where the group had been seen by forest guards, whose accounts were reliable given their familiarity with the terrain and their year-long experience in tracking (and formerly also

hunting) of monkeys from the study group. The grid cell method often produces underestimates of range sizes (e.g. [Sterling et al. 2000; Singleton and van Schaik 2001]. This can be circumvented by including those cells that were not entered by monkeys, but were surrounded by other cells entered into the total home range estimate (thereafter referred to as 'lacunae elimination', e.g. [Albernaz 1997; Kirkpatrick et al. 1998]. We linked isolated cells by connecting them with the minimum number of intervening cells of suitable habitat, and filled lacunae provided they contain supposedly suitable habitat. Three grid cells known to be pastures were not included in the calculation of the home range size even though they were surrounded by cells having been visited by monkeys.

We applied the minimum convex polygon (MCP) for calculation of monthly and seasonal home ranges. Monthly and seasonal home ranges were based on sightings of the study group and finds of fresh scat. Since minimum convex polygons can incorporate large areas that are never used, we adjusted monthly and seasonal polygons (thereafter referred to as 'adjusted polygons'; cf. Chapter 6 in this thesis) by removing unsuitable habitat such as alpine pastures and areas never visited based on our 15-month data set (cf. [Li and Rogers 2005].

We entered GPS readings in longitudes/latitudes for group location into the GIS application ArcView®. We did all subsequent home range analyses with the an extension to ArcView® named YGM (Yunnan Golden Monkey)-TOOL developed by Ruidong Wu, a program that implements a suite of movement and home range analyses functions within the GIS. We edited maps in ArcMap®.

We estimated intensity of utilization by the number of 30-minute location records per grid cell, using GIS. We defined a core area as the sum of all grid cells of the home range that are used more heavily than would result from an uniformly distributed use [Samuel et al. 1985]. Using ArcView®, we recorded daily travel distance as the sequence of coordinates taken at every location record, and calculated the sum of distances between each set of coordinates. Even though we followed the group from morning to evening (ca 0700 – 1900 hr), sometimes the group had changed position between the last sighting of one day and the first sighting of the next. In that case, we apportioned the distance between these sightings on a 50/50 basis and added it to the estimate for the respective days' daily travel distance (*sensu* [Kirkpatrick and Gu 1999].

To predict whether a primate species would be territorial, Mitani and Rodman [1979] devised an index of defendability. This index relates day journey length to the diameter of a

circle equivalent to the home range area. Since no data on mean annual day journey length are available, we used the data obtained from the one-month follow in September 2006.

The degree of human activities and the number of livestock inside the reserve boundaries varied seasonally and are thus bound to have a changing impact on the monkeys' ranging behavior. I noted all sightings of people and livestock inside the home range on tracking days to obtain a crude estimate of how the presence of humans and domestic animals might affect ranging. Since I recorded only those activities detected along the way, we certainly may have missed activities elsewhere, e.g. at elevations above us, that might have affected the animals' movements. I developed a relative index of disturbance to take into account the differential degree of disturbance caused by different human activities and different domestic animals (Tab. 5.1). This is admittedly a somewhat arbitrary classification, but it provides a crude measure of perceived disturbance.

Tab. 5.1. Different values of the disturbance index based on different disturbances caused by humans and livestock.

Origin of disturbance	Disturbance index	Rationalization
1 dog	2	Sound of barking is far-reaching, and dog comes closest to a natural predator
1 person of which activity/purpose could not be determined	1	Less than 'dog' because partial habituation to humans has been achieved
1 person cutting tree	1.5	Noise of wood chopping makes disturbance higher
1 person looking for medicine, mushrooms	1	More unobtrusive activity than tree cutting
1 cow in forest	0.5	Higher than 'cow on meadow' because forest habitat is shared by golden monkeys
1 cow on meadow	0.25	Lower than 'cow in forest' because meadows are usually not visited by monkeys
1 sheep in forest	0.25	Lower than 'cow in forest' because of smaller size and less damage in terms of food consumption/vegetation destruction

There are no comparable direct measures of habitat quality at different *R. bieti* study sites. However, habitats can be divided simply into marginal and productive ones. Features of marginal habitats as opposed to more productive ones are: lower temperature, less rainfall, lower species diversity, higher elevation, and poorer soils. Based on these criteria, Tibet (Xiaochangdu) and Baimaxueshan North (Wuyapiya) comprise marginal habitats while Baimaxueshan South (Samage) as well as Jinsichang, Longma and Fuhe comprise relatively productive habitats [Long et al. 1994; Xiang et al. 2007a]. The marginal sites lie at latitudes

above 28˚30'N, while the productive sites lie at latitudes below 27˚36'N. Using ANCOVA, I tested for a relationship between productivity (productive vs. marginal) and log-transformed home range size (dependent variable) while including log-transformed group size as a covariate.

I performed statistical procedures in SPSS 12.0. Tests for significance were two-tailed. Seasons were classified as spring (Mar-May), summer (Jun-Aug), Fall (Sept-Nov) and winter (Dec-Feb). I used the following data sets for analyses: calculation of total home range size: September 2005-November 2006; calculation of seasonal home ranges: September 2005-August 2006; relation between phenology and home range size: November 2005-October 2006 (since phenological records for September/October 2005 were incomplete).

Phenology

To assess abundance of different tree species, we quantitatively inspected and identified 1851 individual trees in 67 20x20 m botanical plots within the study group's home range. For details on vegetation assessment, see Chapter 4 in this thesis. Of these 1851 marked trees, 307 trees were selected for monthly phenological monitoring, and another subset of 157 trees from 21 genera known to contribute significantly to the diet (Chapter 8 in this thesis) was then selected for the analyses presented in this paper. These latter phenological records were intended to characterize seasonal changes in the availability of *R. bieti* food resources. Trees selected for phenological monitoring were mature individuals with girth over 40 cm that offered a good view of their crowns. We conducted phenological sampling at monthly intervals, when we visually inspected each marked tree, and recorded the presence of fruits, flowers and young leaves. We calculated the proportion of monitored trees bearing each of the phenophases every month (cf. [Yeager 1989a; Li 2006]).

Results

Home Range Size and Temporal Variability

The focal *R. bieti* group entered 269 grid cells (16.81 km^2) over 14 ½ months in 2005/2006 (Fig. 5.1). We saw the group in 205 of these map cells, and detected signs of their presence, i.e. faeces, remnants of discarded food and prints, in an additional 64 map cells. 24.75 km^2

(396 grid cells) represents the total home range estimate after including grid cells surrounded by visited cells (lacunae) and linking isolated grid cells. Applying a correction factor for terrain resulted in a final home range size estimate of 32.31 km^2. For comparative purposes, the annual home range size would be 21.25 km^2 (27.7 km^2 with correction for terrain).

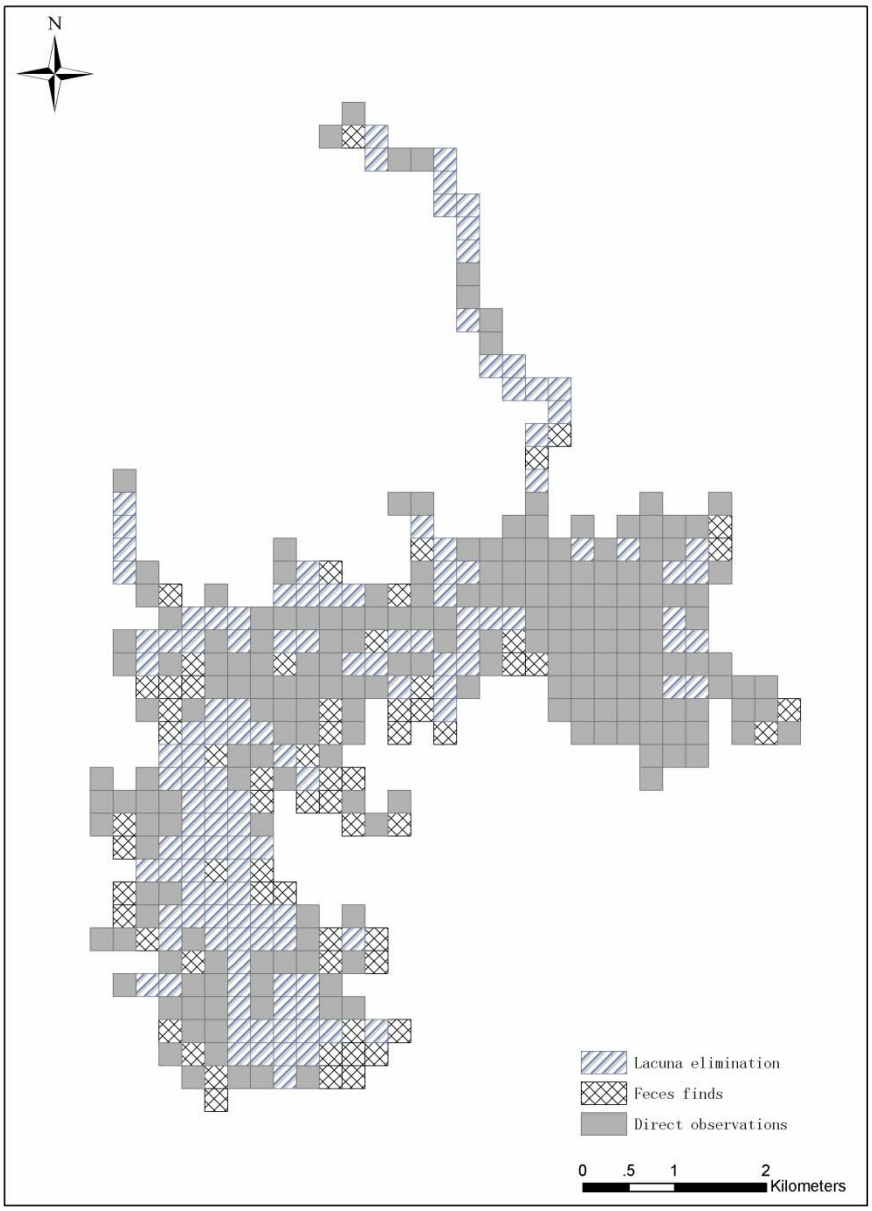


Fig. 5.1. Total home range of the Gehuaqing band of *R. bieti* at the Samage Forest, Baimaxueshan Nature Reserve in 14 ½ months (September 2005-November 2006). The figure contains not only grid cells where we spotted the group, but also grid cells where we found faeces and grid cells surrounded by visited cells.

The cumulative number of new grid cells visited by the study group with each successive month is displayed in Fig. 5.2. The group continually entered new grid cells, and the curve had not yet reached an asymptote by October 2006; however, additional data collected by field assistants in November and December 2006 indicated that the focal band did not venture into new areas. Nevertheless, the group has occasionally made excursions into peripheral areas in previous years. Including those areas where forest guards have seen the band in the previous ten years (1996-2005), the size sums up to 43 km^2 (56.1 km^2 with correction for slope).

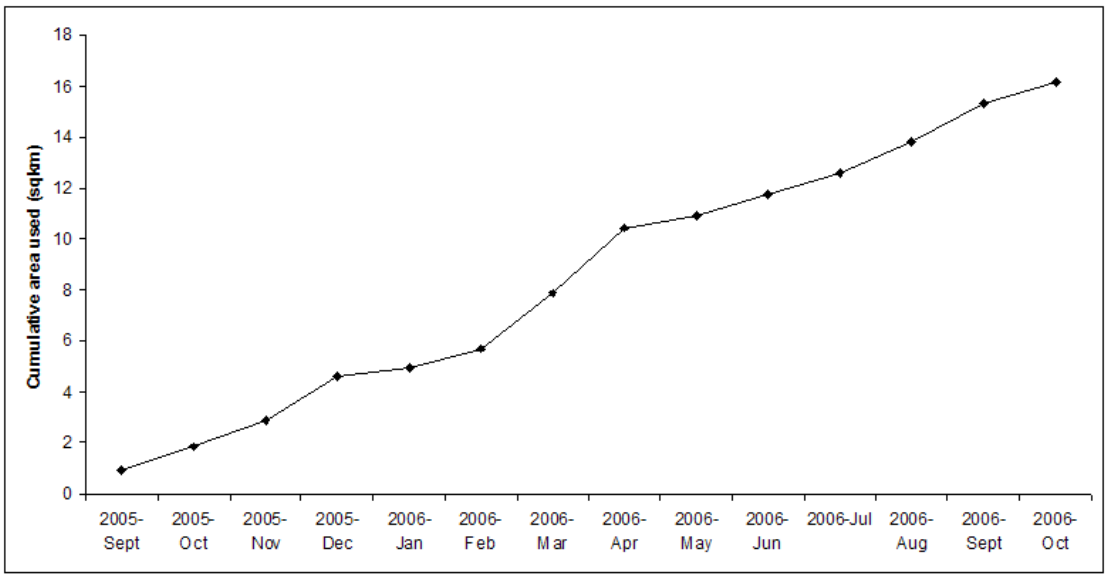


Fig. 5.2. Cumulative increase of the home range of the Gehuaqing band, based on group sightings (i.e. location records) and finds of faeces.

Sampling effort was uneven among months, ranging from four days of observation in January to 17 days of observation in August (Tab. 5.2). However, there was neither a significant correlation between the number of observation days per month and monthly home range size (Spearman rank correlation, r_s = .477, p = .117, *n* = 12 months) nor between monthly number of location records and monthly home range size (r_s = .343, p = .275, *n* = 12 mo), implying that the uneven sampling effort only marginally affected data comparability and interpretation.

Tab. 5.2. Number of location records and observation days per month as well as monthly home range estimates (based on the adjusted minimum convex polygon method) for the *R. bieti* band in the Samage Forest.

Month	Observation days	Location records	Adjusted MCP[a] [km^2]
Sep 2005	9	55	5.13
Oct 2005	10	107	1.27
Nov 2005	7	76	7.36
Dec 2005	14	90	5.83
Jan 2006	4	40	0.73
Feb 2006	6	42	5.13
Mar 2006	12	120	8.95
Apr 2006	16	124	12.77
May 2006	12	89	1.75
Jun 2006	9	53	14.52
Jul 2006	14	83	6.03
Aug 2006	17	103	10.48
Sep 2006	30	505	6.51
Oct 2006	15	107	9.7
Nov 2006	9	104	NA
Total	184	1698	NA

[a] Not corrected for slope.

The mean monthly home range area of *R. bieti* based on the adjusted minimum convex polygon method was 6.7 km^2. Polygon-based sizes of seasonal and monthly and also home ranges varied considerably (Tab. 5.2). Spring home range was 17.8 km^2, summer home range 18.6 km^2, fall home range 9.3 km^2, and winter home range 18.2 km^2 (Fig. 5.3).

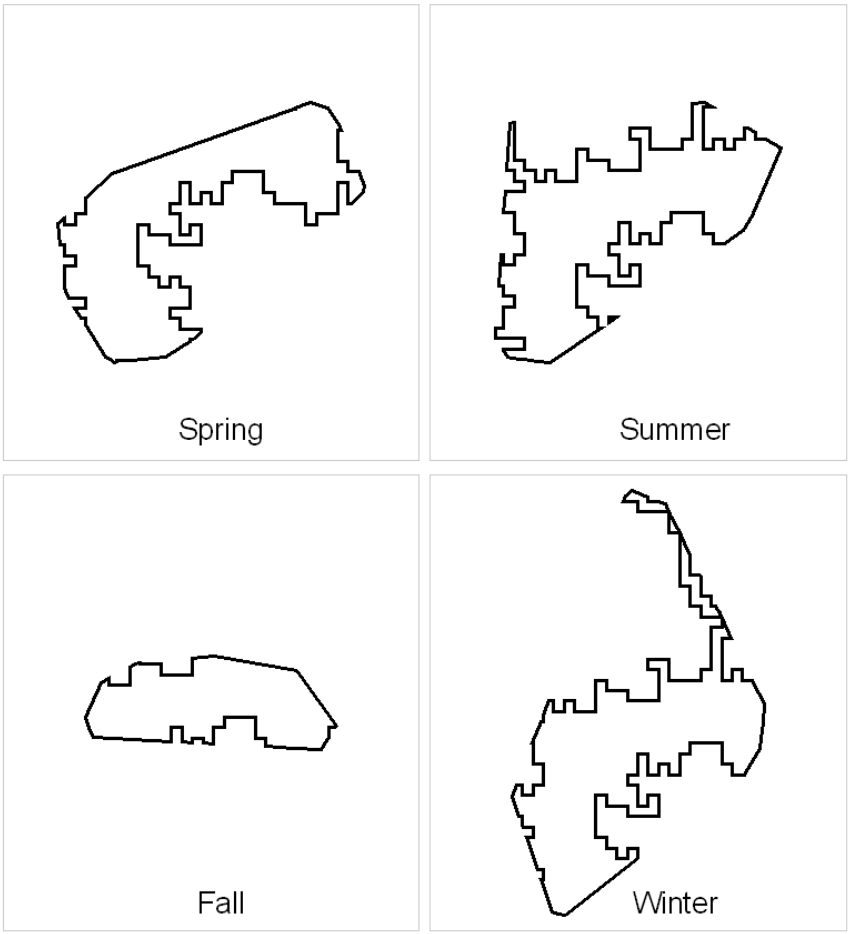


Fig. 5.3. Adjusted minimum convex polygons of seasonal home ranges of *R. bieti* at Samage. I excluded unsuitable and never visited areas from the polygon.

Intensity of use of grid cells varied markedly. Many cells were entered only once, whereas others had up to 64 location records. The difference between the observed and expected distributions of location records across the home range was highly significant (Kolmogorov-Smirnov 1-sample test, $Z = 9.199$, $p < .001$, $n = 205$). Range use of *R. bieti* surpassed the expected uniform distribution in 60 'core' cells (29.3% of all grid cells with location records; Fig. 5.4). These cells constitute a core zone, albeit not a contiguous one. 50% of all location records occurred in only 29 cells, which corresponds to 1.81 km^2. 75% of all location records occurred in 69 cells, which corresponds to 4.31 km^2 (Fig. 5.5).

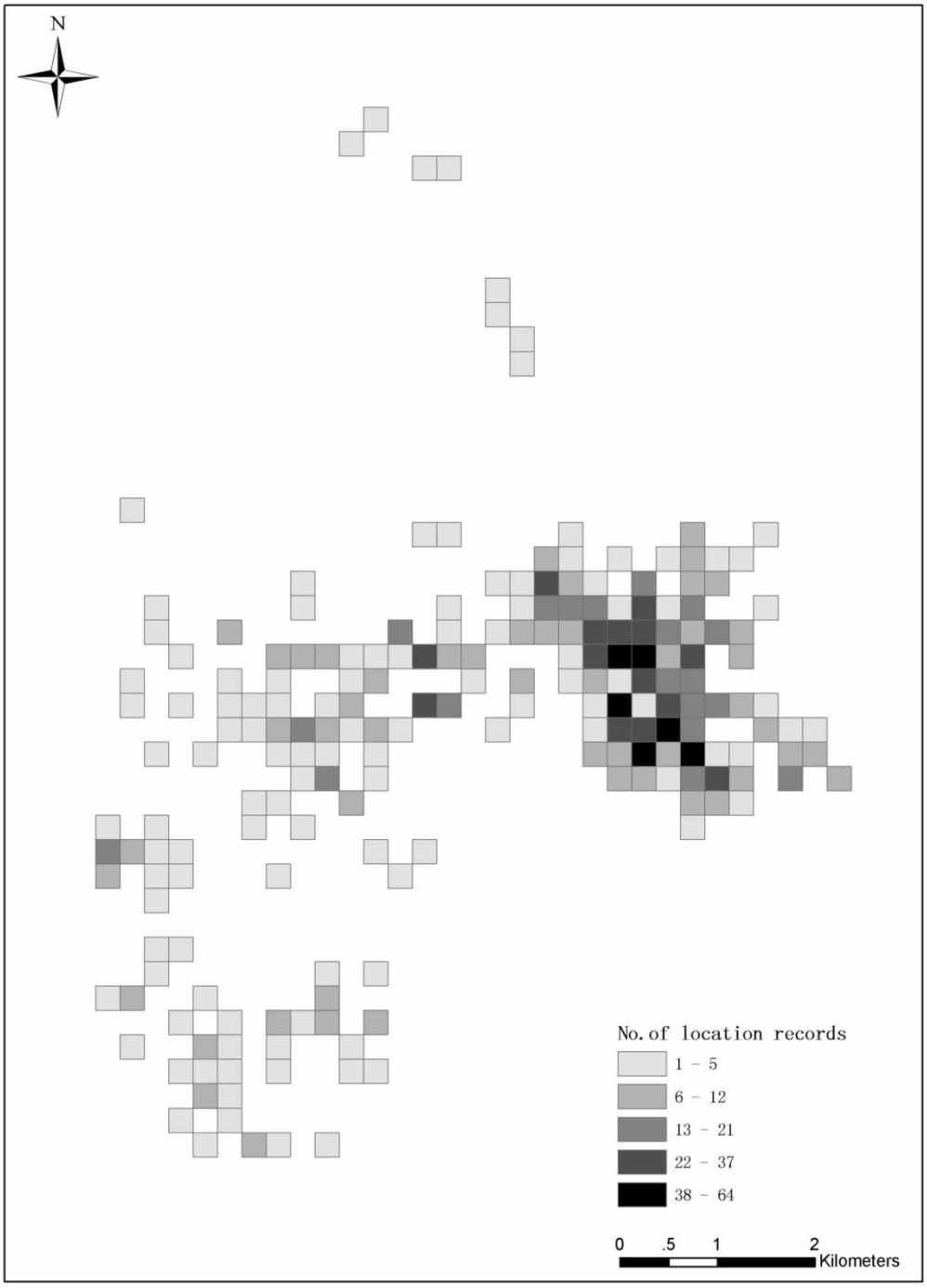


Fig. 5.4. Total home range of *R. bieti* at Samage. Parts of their range were obviously utilized in an uneven manner. The eastern part was used frequently, whereas the western and southwestern part was used less frequently. The northern part was used only once when the group made an excursion. Darker tones indicate a higher number of location records, i.e. more frequent use.

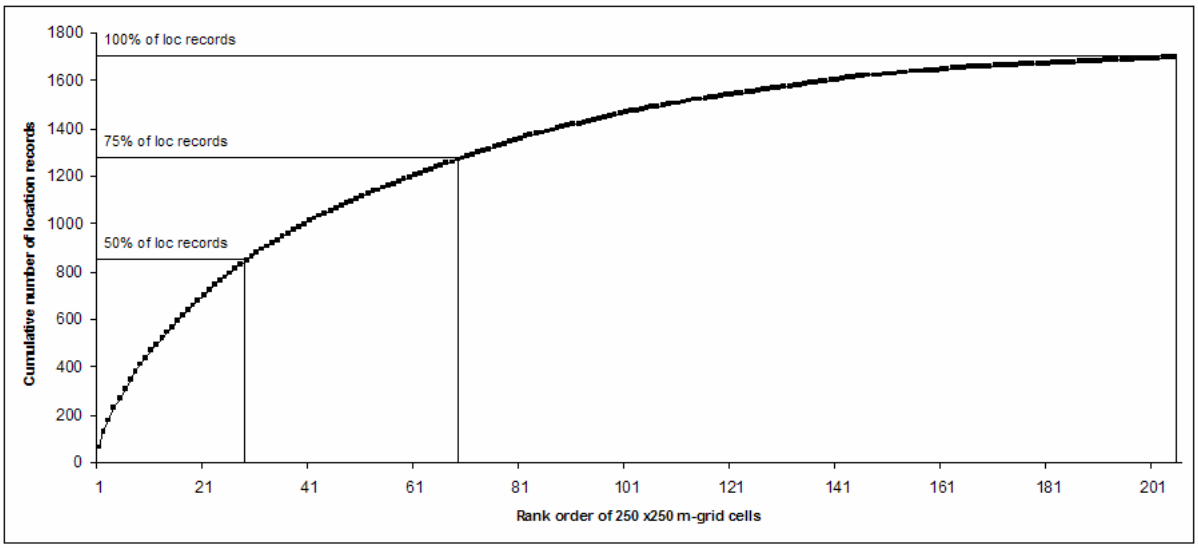


Fig. 5.5. Cumulative number of location records of the Gehuaqing band in 250 m grid cells. Cells are arranged in rank order of use. The areas accounting for 50, 75 and 100 % of all location records are designated.

Correlates of Range Use

Availability of new leaves, flowers and fruit varied across the annual cycle (Fig. 5.6). Fruit abundance reached a peak in August, and we recorded a flush of immature leaves in May. We did not find any significant correlations between presence of young leaves and monthly range size (r_s = .312, p = .324, *n* = 12 mo), presence of fruits and monthly range size (r_s = .277, p = .384, *n* = 12) and presence of flowers and monthly range size (r_s = .120, p = .710, *n* = 12).

Monthly home range size was neither significantly correlated with the number of people (r_s = .411, p = .185, *n* = 12 mo) nor the total disturbance index (r_s = .340, p = .280, *n* = 12) (Tab. 5.3).

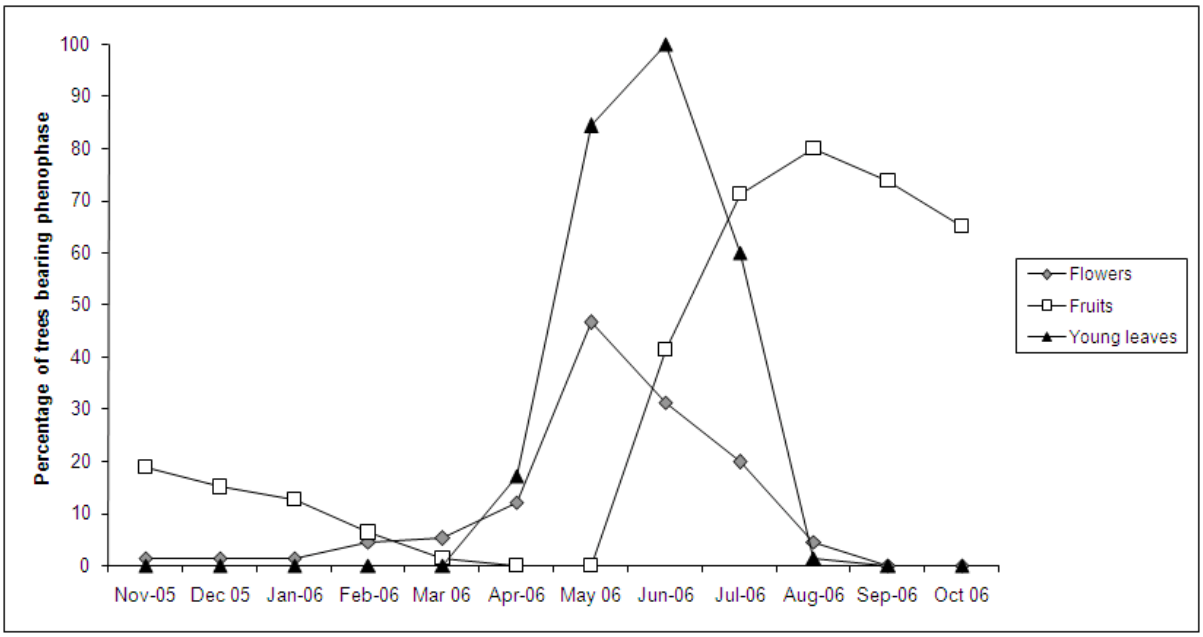


Fig. 5.6. Availability of fruits, young leaves, flowers of *R. bieti* food trees at the Samage Forest, South Baimaxueshan Nature Reserve in 2005/2006. Data come from 157 sampled tree specimens. According to our phenological data, fruit availability is meager in winter, but this finding may be due to the fact that our phenology trees lie within the heavily utilized core area of the band where fruit resources became almost depleted. Some trees outside the core areas still bore fruit in late winter (pers. obs.).

Tab. 5.3. Average number of people encountered per day for each month and total monthly disturbance index. The latter is derived from an evaluation of different human activities and different domestic animals.

Month/season	No. of people	Total disturbance index
Sep 2005	3.3	6.8
Oct 2005	0.6	2.15
Nov 2005	0.7	3
Dec 2005	0.2	1.2
Jan 2006	0.7	0.7
Feb 2006	0	0
Mar 2006	1.2	1.4
Apr 2006	4.1	5.05
May 2006	5	9.65
Jun 2006	2.7	5.9
Jul 2006	2.2	2.9
Aug 2006	6.2	9.55
Fall 2005	1.7	4.2
Winter 2005/06	0.1	0.8
Spring 2006	3	4.3
Summer 2006	3.5	5.3

There were no significant correlations between monthly range size and temperature (r_s = .339, p = .282, *n* = 12 mo) or between monthly range size and rainfall (r_s = .109, p = .737, *n* = 12; climate data in Chapter 4 in this thesis). Monthly variation in day length was not associated with variation in monthly home range sizes (r_s = .473, p = .121, *n* = 12) (Fig. 5.7).

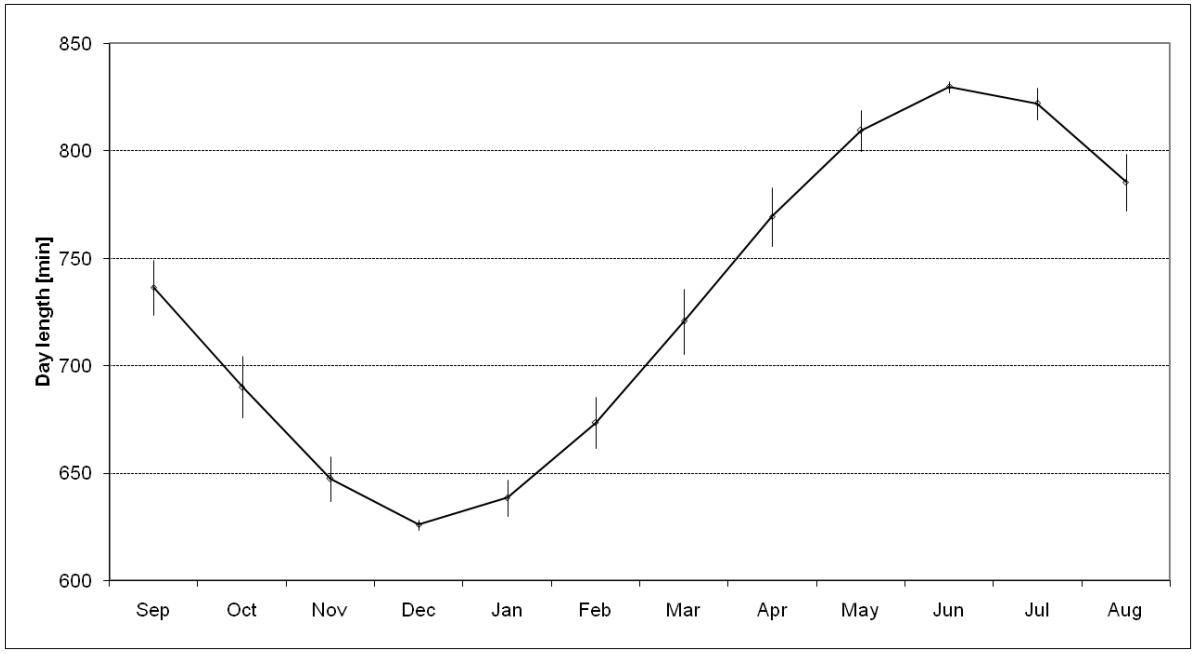


Fig. 5.7. Day length variation among months for the study site in Weixi County, Yunnan Province, PRC. Standard deviations are shown as vertical lines.

Daily Moving Distance Based on Full-Day Follows

There was a conspicuous variance in daily travel distance in September 2006. The band showed concentrated use of certain confined areas and short daily travel distances (<1500 m) for three consecutive days twice that month. On the days before and after these relatively stationary phases, the band engaged in long distance travels of >1500 m (Fig. 5.8). The mean daily travel distance in September was 1620 m (range 578 – 4216 m, SD = 798 m) (Fig. 5.9). The largest elevational range covered in one day was 400 m. Overall movements in that month were characterized by a zigzag pattern with frequent returns to previously visited areas. Distances travelled fluctuated with day-time. There were three peaks of travel

(10:30-11:30, 13:30-16:30, 18:30-19:30) and three periods of relative immobility (06:30-09:30, 11:30-13:30, 16:30-17:30).

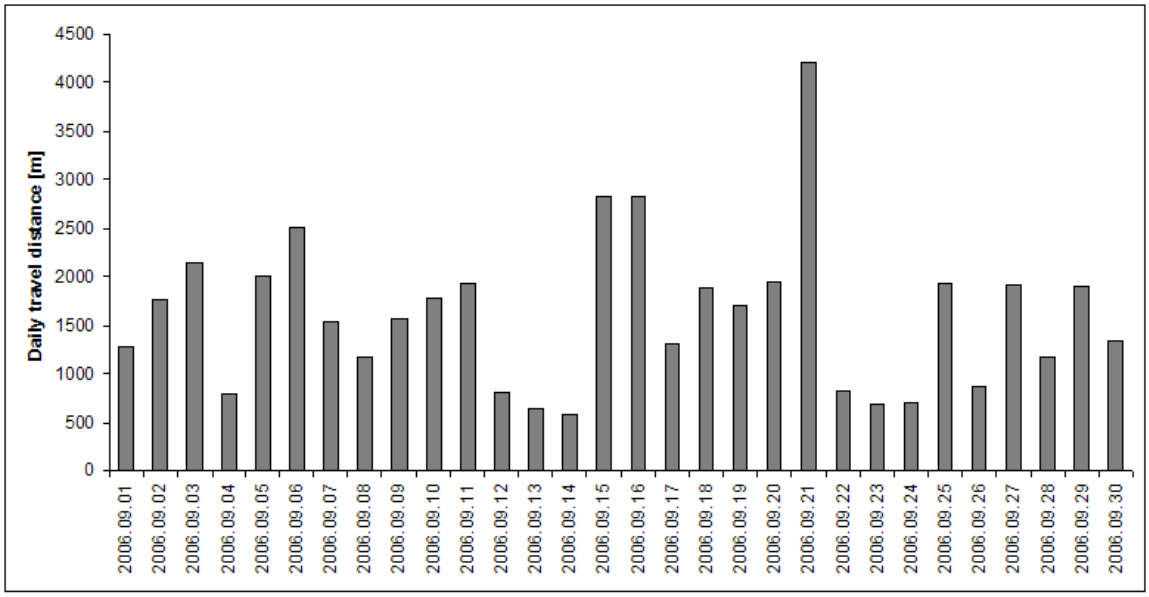


Fig. 5.8. Daily travel distance of the Gehuaqing group in Sep 2006. The long distance on Sep 21 may be erroneous and may have been caused by falsely following a splinter group from the main band.

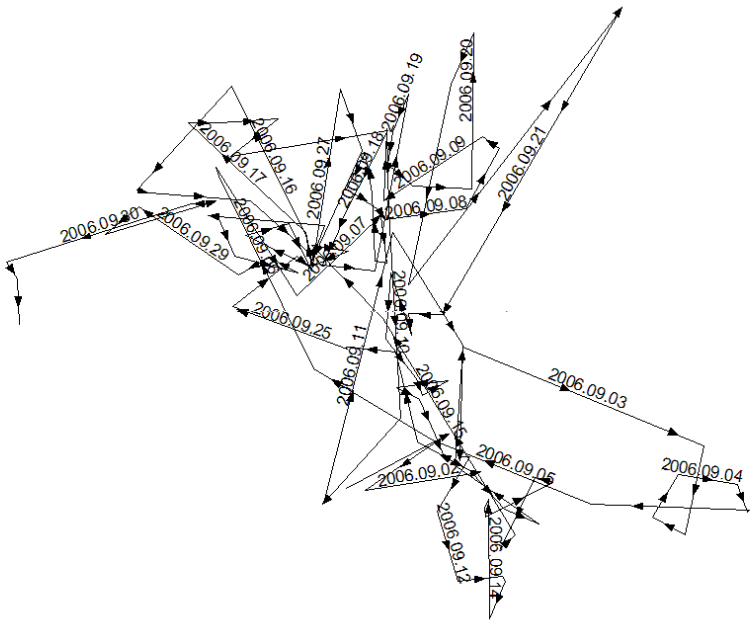


Fig. 5.9. The daily travel distances of Fig. 5.8 put in a directional context. Arrows indicate direction of travel. Dates are indicated.

Territoriality and Home Range Overlap between Bands

A comparatively low index of defendability of the Gehuaqing group at Samage (0.29; 0.25 if the home range estimate corrected for slope is applied) suggests that the group is unable to defend an exclusive territory (Mitani and Rodman, 1979). We found indirect evidence of another small group (Shikuadi) that partially shared the same space, but difficult observation conditions and lack of individual identification made it impossible to clearly identify inter-group encounters.

Relation between Group Size, Home Range and Productivity

Table 5.4 gives data on group size and home range size of all groups of *R. bieti* studied at the various sites. Using ANCOVA, I tested for a relationship between productivity (productive vs. marginal) and home range size (dependent variable) while including group size as a covariate. Since the interaction group size*productivity did not have a significant effect on home range size ($p = .162$), I then calculated the ANCOVA model without the interaction effect. Group size had a significant positive effect on home range size ($F = 33.176$, $p = .010$, $df = 1$). I found a trend toward larger home ranges in marginal habitats: productivity did have a nearly significant effect on home range size ($F = 8.439$, $p = .062$, $df = 1$).

Tab. 5.4. Group size and home range size of all studied groups of *R. bieti*.

Site	Group size	Home range size [ha]	Notes	Geographical distribution[a]	Reference
Fuhe	80	1070	250 x 250 m grid used; group size approximate; data obtained during an unspecified number of months over a 1¼-year period	S	[Liu et al. 2004]
Jinsichang	180	1730	250 m x 250 m grid used; group size approximate; data from 11 continuous months	S	Ren et al. in prep
Longma	80	956	250 m x 250 m grid used; group size approximate; data from 14 more or less consecutive months	S	[Huo 2005]
Samage	410	2475[b]	250 m x 250 m grid used; data from continuous 14½ months	M	This study
Wuyapiya	175	2525	500 x 500 m grid used; data from 12 months over 2 years	N	[Kirkpatrick et al. 1998a]
Xiaochangdu	210	2125	500 x 500 m grid used; data from 13 months over a 22-month period	N	[Xiang 2005a]

[a] S = southern part of the geographical range of *R. bieti*, M = middle part, N = northern part.

[b] Estimate not corrected for slope to ease comparability.

Discussion

Temporal Variability in Ranging

In many cases, temporal variation in primate range use is related either to utilization of valuable rare localized resources and/or major food items [Fashing 2007]. Major diet components clearly influence ranging in Ugandan red colobus (*Piliocolobus tephrosceles* [Clutton-Brock 1975]), Tana River red colobus (*Piliocolobus rufomitratus* [Marsh 1981]), *Colobus satanas* [McKey and Waterman 1982; Fleury and Gautier-Hion 1999], king colobus (*Colobus polykomos* [Dasilva 1989]), white-thighed surilis (*Presbytis siamensis* [Bennett 1986]), southern plains gray langurs (*Semnopithecus dussumieri* [Newton 1992]), maroon leaf monkeys (*Presbytis rubicunda* [Davies 1984]), capped langurs (*Trachypithecus pileatus* [Stanford 1991a]), white-bellied spider monkey (*Ateles belzebuth* [Nunes 1995]) and mountain gorillas (*Gorilla beringei beringei* [Watts 1998b]). However, for several populations, range use is not clearly related to these primary dietary variables [Struhsaker 1974; Oates 1977; Fashing 2001a; Sangchantr 2004], but seem to be more affected by scarce resources, e.g. swamp plants and eucalyptus bark in *Colobus guereza* [Oates 1978; Fashing 2001a; Fashing et al. 2007a; Harris and Chapman 2007], saltlicks in Phayre's leaf monkey (*Trachypithecus phayrei* [Pages et al. 2005]), and water in hamadryas baboons (*Papio hamadryas* [Zinner et al. 2001]. We detected no statistical relationship between monthly availability of main food items and home range size of the Gehuaqing band. Nevertheless, it is still possible that a careful fine-grained, albeit logistically challenging, study of the band's daily travel distance would reveal positive correlations between monthly availability of food and daily travel distance. Moreover, monthly consumption of fruit (as opposed to monthly availability) may have an effect on range use. Two findings from this study, i.e. the substantially smaller home range in fall and the large winter home range, were unexpected and require explanation.

Large Winter Home Range

A relatively large area was covered by the *R. bieti* group at Samage in winter. Other studies on *R. bieti* at more northern localities, conversely, documented a reduction in home range size and/or daily travel distance in winter [Kirkpatrick et al. 1998; Xiang 2005]. Data

on monthly variation in daily travel distance are not (yet) available for Samage, but the size of the home range remained large in winter. This dichotomy might best be explained by the unequal availability of food resources in winter at different study sites. Climate is more adverse at Wuyapiya and Xiaochangdu at the northern tip of Yunnan and food diversity is more restricted in comparison with Samage. Two likely reasons for the absence of a smaller winter home range at Samage are discussed below.

At Samage, only 0.2% of all investigated trees were assigned the lichen-load category 'heavy' whereas at Wuyapiya 29% of the trees had 'heavy' loads of *Bryoria* lichens (for a definition of lichen load categories, see [Kirkpatrick 1996] and Chapter 4 in this thesis). Thus, the relatively lower abundance of lichens may force the Gehuaqing band to cover wider areas in search of them whereas there is no need for the Wuyapiya band to travel far since lichens are abundant and other high-quality food items are out of reach or in negligible supply.

The large winter range was partly a result of an excursion, i.e. visit to peripheral areas of the home range, and partly a result of traveling extensively to pursue the last remaining fruits. At Samage, the spatial distribution of arboreal fruit appeared to have changed from fall to winter after natural abscission and after fruit depletion in some areas had taken place. Our phenology data show that, out of 157 fruit trees, we found fallen fruit beneath only 23 individual trees in November 2005, 27 trees in December 2005 and 20 trees in January 2006 (we did not detect any fallen fruit in October 2005). The fact that we found surprisingly few fruits beneath trees implies that they had been eaten beforehand (fallen fruits decompose slowly in the dry season). We witnessed on several occasions that the phenology fruit samples were fed on by the monkeys and assume that after intense foraging in the most fruit-rich core areas of the band's range in fall, fruits had to be actively sought out in winter. Extensive ground surveys revealed that some trees in more remote areas (which were visited by the band in winter) were still largely covered with preferred fruits such as *Sorbus* spp. (Rosaceae) and *Acanthopanax evodiaefolius* (Araliaceae) even in late winter. The higher costs of long travels associated with searching for fruit may be compensated for by the presumably high nutritional and energy returns content of the fruits.

Home Range Reduction in Fall

In fall, when fruits were plentiful and constituted a major part of the diet, the *R. bieti* band at Samage displayed more concentrated and restricted range use. When favorite fruit tree species are relatively abundant and spatially clumped in the home range, a primate group can economize on the time and energy of travel by intensively exploiting the resource within a small portion of its home range [Iwamoto 1992; Kaplin 2001; Terborgh 1983; Fashing 2001a]. In the Samage Forest, the key fruit species in the diet of *R. bieti* - *Acanthopanax evodiaefolius*, *Sorbus thibetica*, *Sorbus* spp., *Cornus macrophylla* (Cornaceae) (Chapter 8 in this thesis) - occurred at relatively high densities and showed overall synchrony in their fruiting patterns, thus enabling the band to feed largely on fruit within relatively small areas. The home range in fall was the smallest. In September, the group criss-crossed a relatively confined area and showed high return frequencies to previously visited areas. Such zigzagging may lead to increased daily travel distance, but not necessarily to increased monthly home range. Others have made similar observations: the spatially concentrated distribution of acorns, a seasonally preferred and ample food item for *Rhinopithecus roxellana* in the Qinling Mountains and *Semnopithecus schistaceus* at Simla, resulted in small ranges in fall [Sugiyama 1976; Guo 2004; Tan et al. 2007]. We expected the Gehuaqing group to exhibit similarly concentrated use of space in summer when fruit availability reached a peak, which most likely would have produced a significant correlation between fruit availability and seasonal range sizes. The co-occurrence of juicy bamboo shoots in summer, which appeared in spatially separated patches, caused the group to move far and may have masked a statistical effect of fruit availability on range size.

Fluctuating Daily Travel Distances

Our limited data set on daily travel distance demonstrates that the focal *R. bieti* group has among the longest day journey lengths of all leaf monkeys [Fashing 2007; Kirkpatrick 2007], and that the group alternated between short-distance and long-distance travels. Kirkpatrick et al. [1998] also observed that *R. bieti* show concentrated utilization of areas of 1 to 2 km^2 for about one week, at which time they proceeded 2-6 km to another area of concentrated utilization. Alternating between long distance movements and concentrated use has also been reported for *Colobus satanas* [Fleury and Gautier-Hion 1999]. Along the same

lines, *Semnopithecus schistaceus* has been found to follow a pattern of "sweeps and concentrations", using only segments of their nearly continuous forest intensively and interspersing these periods with sweeps of the entire range [Bishop 1975; Bishop 1979]. A comparable pattern is also prevalent in Tibetan macaques (*Macaca thibetana*) and Japanese macaques (*Macaca fuscata*) which have been observed to forage within the group's most densely utilized areas for several days after which they move to more distant and less used areas/food patches ("wandering and tripping") [Wada and Tokida 1981; Zhao and Deng 1988].

Why such a Large Home Range? - Intra-specific Comparisons among Sites

The golden monkeys' peculiarity of having extraordinarily large home ranges had already emerged from small-scale studies of Chinese scholars in the 1980s (e.g. [Wu et al. 1988]). Large range sizes have subsequently been discovered at all study sites of all Chinese *Rhinopithecus* species (e.g. [Bleisch et al. 1993; Kirkpatrick et al. 1998; Su et al. 1998; Kirkpatrick and Gu 1999; Li et al. 2000; Guo et al. 2004; Xiang 2005]. Home ranges of this magnitude are usually found only in ground-dwelling primates living in open environments such as in anubis baboons (*Papio anubis*) (e.g. [Barton et al. 1992]; 44 km^2), savanna chimpanzees (*Pan troglodytes*) (e.g. [Baldwin et al. 1982]; >50 km^2), *Papio hamadryas hamadryas* (e.g. [Swedell 2002b]; 30 km^2), and patas monkeys (*Erythrocebus patas*) ([Enstam and Isbell 2007]; 40 km^2). In line with Kirkpatrick et al. [1998], the home range of the Gehuaqing band of black-and-white snub-nosed monkeys is one of the largest home ranges ever documented for a primarily tree-dwelling primate. Among the few other truly wide-ranging arboreal primates are male Sumatran orangutans (*Pongo abelii*) ([Singleton and van Schaik 2001]; >25 km^2) and Rwandan *Colobus angolensis* ([Fashing et al. 2007b]; 24 km^2).

The home range estimate of 32 km^2 presented here is based on data from roughly 15 months. The larger estimate of roughly 56 km^2 is due to rare excursions into peripheral areas and is largely based on accounts of reserve staff and former hunters. Similarly, Kirkpatrick et al. [1998] found the home range of the Wuyapiya band to be 25 km^2 over a period of 2 years, but they state that the band may have covered >100 km^2 within a decade. The question arises why these monkeys have such extremely large home ranges.

Several studies have discovered negative correlations between range size and habitat quality or productivity (e.g. *Macaca mulatta* [Jiang et al. 1991]) or have found range size to be larger in areas of poor habitat quality (e.g. *M. sylvanus* [Mehlman 1989], *Semnopithecus* spp. [Bishop 1979], forest vs. savanna chimpanzees [Baldwin et al. 1982; Herbinger et al. 2001]). Our results indicate a statistical trend toward larger home ranges of those *R. bieti* groups living in high-altitude cold depauperate habitats in the north as opposed to those living in low-lying warmer and productive habitats in the south. This effect would be highly significant without inclusion of the present study at Samage that - contrary to expectations - found a very large home range in a fairly productive environment.

Within-species variation in habitat structure and resource availability offers a likely explanation for the unexpectedly large home range at Samage. This home range is configured to include a patchwork of fairly distinct vegetation types of which only the mixed forest appears to be of any significance in terms of resource procurability and is utilized on a regular basis by *R. bieti* [Chapter 4 in this thesis]. Patches of fruitful mixed forest are interspersed with other vegetational strata such as pine forest, oak forest and fir forest, and this may automatically lead to an enlargement of the home range since the band has to cross these less desired other forest types to reach their preferred forest type. Home range is thus expected to be larger where such fruitful patches are fragmented and dispersed (*sensu* [Geffen et al. 1992]).

Besides habitat heterogeneity, large group size appears to be another main factor that accounts for the overall large home range of *R. bieti*. A positive correlation between group size and home range size or group size and daily travel distance has been found in several primate taxa (e.g. [van Schaik et al. 1983; Barton et al. 1992]). An increase in the size of a group causes a larger biomass per unit area. To sustain per capita energy intakes, the quantity of available resources must be enlarged. We would thus anticipate that as group size increases there should be a corresponding increase in home range size (cf. [Nunn and Barton 2000]). Similarly, the enlargement of a group may necessitate increased travel to counter deficits in food supply. If such positive associations are present, as found in this study for *R. bieti*, they are an indication of scramble competition [Chapman 1990; Isbell 1991; Janson and van Schaik 1988].

Compared to other monkeys, evidence for intragroup scramble competition is less straightforward in colobines because their often relatively abundant and evenly spaced food supply may diminish scramble competition and not impose larger daily travel distances (e.g.

[Fashing 2001a]). For instance, in *Piliocolobus tephrosceles*, there is no correlation between group size and daily travel distance [Struhsaker and Leland 1987]. In Asian colobines as a whole, there is neither a positive correlation between daily path length and group size nor between home range size and group size [Yeager and Kirkpatrick 1998], implying that intragroup scramble competition seems to be of minor importance in these species (but see Chapter 1 in this thesis). However, others found a positive relationship between group size and daily travel distance (e.g. [Steenbeek 1999a]). Another reason scramble competition may be hard to identify in colobines is that ranging behavior may be influenced by irregularly distributed and scarce mineral-rich resources which may force some groups to travel long distances to exploit these, while others who live closer do not have to travel as far [Fashing et al. 2007 b; Harris and Chapman 2007].

Kirkpatrick [1996] assumed that reliance on slow-growing lichens, the prime feeding resource of *R. bieti*, dictates range utilization in the temperate and very seasonal forests of Wuyapiya to a considerable degree. Since lichens need years or even decades to regenerate after consumption [Wu 1987; Kirkpatrick 1996], it is hypothesized that the monkeys need an extensive home range and forage semi-nomadically to avoid depletion and allow overutilized patches recover (see also [Kirkpatrick and Gu 1999]). Similarly, Watts [1991] proposed that mountain gorillas may harvest fibrous foods in such a way as to replenish the food supply and return later to the same site after regeneration has taken place. Compared to mountain gorillas, renewal rate is much slower for lichens than for herbaceous vegetation. Hence, if the snub-nosed monkeys' strategy is allowing lichens to regrow to a harvestable length, they have to abandon areas for a decade or more. This is clearly not found in this study. Our observations indicate that the *R. bieti* band returns to particular areas after several months of absentia (not years or decades). If the habitat was less fragmented, the band would possibly leave patches for a decade or more to allow lichen renewal to take place. At the moment, the monkeys still seem to have sufficient quantities of their dietary staple left, but sustained consumption exceeding production would result in a decreased standing crop and may create dietetic problems in the future.

Home Range Overlap, Core Area and Site Fidelity

Based on the Mitani-Rodman index, the Gehuaqing group is theoretically not capable of territoriality. No territorial encounters were observed. It is practically challenging to verify

whether other neighboring bands have overlapping home ranges with the focal band, but partial home range overlap has been inferred for our focal group at Samage. This is in accord with findings for the *Rhinopithecus roxellana* bands at Shennongjia [Ren et al. 2000] and at Zhouzhi [Tan et al. 2007].

The Gehuaqing band used large parts of their range only very infrequently. Some grid squares, however, were used very often. Outlying peripheral areas were visited only once or twice over the whole study period. This resembles the range use strategy of Eastern gorillas (*Gorilla beringei*) which use their entire home range only on a long-term basis and limit their range to small fractions of their home range in any given week or month [Vedder 1984; Yamagiwa et al. 1996]. Differential intensity of home range use has also been noted by Kirkpatrick et al. [1998] and Liu et al. [2004]. In case of the group at Mt. Fuhe, the frequently used grid squares were usually the ones including sleeping sites [Liu et al. 2004]. The core cells of the *R. bieti* group at Samage are not continuous, and occur in patches across the band's home range. The discontinuous nature of the core cells is best explained by the heterogenous nature of vegetation distribution across the home range.

Some groups of *Rhinopithecus* were witnessed to show large-scale home range shifts. The central core of the Wuyapiya band's range for example appears to have moved 8-10 km over a decade [Kirkpatrick et al. 1998], apparently because of a rise in mushroom collection and forest contamination after insecticide spraying among other factors [MacLennan 1999; Forest Biodiversity Database System (中国林业可持续发展信息网) 2006]. At Shennongjia, road construction caused a band of *R. roxellana* to avoid a previously regularly utilized area [Su et al. 1998]. In the Qinling Mountains, logging operations are most likely responsible for the observed change of the summer home range of a band of *R. roxellana* [Li et al. 1999]. The Gehuaqing band seems to have exhibited site fidelity for decades (Shunkai Feng, pers. com.) with the exception of short-term forays into remote corners of their home range on rare occasions, suggesting that bands do not shift home ranges, unless forced by disturbance.

Past commercial logging had a highly disruptive effect on the physiognomy of the Samage Forest. Broad areas were cleared as a result of large-scale commercial logging operations in adjoining Deqin County, which rendered this area uninhabitable. If the habitat across the county border was still largely intact, it seems reasonable to assume that the group's home range would be wider and its pattern of ranging even more migratory.

CHAPTER 6 - Choice of an Analytical Method Can Have Dramatic Effects on Primate Home Range Estimates

Introduction

Various analytical techniques exist to quantify home ranges of non-human primates, and each technique has its strength and limitations. By far the most commonly applied methods are the grid cell method and the minimum convex polygon (MCP) method. Using the grid cell method [White and Garrott 1990; Adams and Davis 1967], the area the study group has traversed is dissected by a grid of cells or squares, and the sum of the grid cells with associated positional records provides an estimate of home range size. The grid cell method often produces underestimates of range sizes (e.g. [Sterling et al. 2000]). On the other hand, the grid cell method may also overestimate home range size because it is highly affected by the size of the grid squares employed (e.g. [Kool and Croft 1992; Lehmann and Boesch 2003]).

An MCP is constructed by connecting the outer locations to form a convex polygon, and then the area of this polygon is calculated [Harris et al. 1990; Hayne 1949; White and Garrott 1990]. The drawbacks of this method are manifold: MCPs provide only crude outlines of primates' home ranges, generally overestimate home range area, are highly sensitive to outliers (i.e. effect of excursions), can incorporate large areas that are never used etc. [Burgman and Fox 2003; Ostro et al. 1999; Powell 2000].

My methodological comparison demonstrates that the choice of a particular analytical technique can have substantial consequences on the respective home range estimates. This is exemplified by a recent data set on black-and-white snub-nosed monkeys (*Rhinopithecus bieti*).

Methods

Data were collected on a partially habituated group of *R. bieti* at South Baimaxueshan Nature Reserve (27°34'N, 99°17'E) over a period spanning 15 months (Sep 2005 – Nov 2006). The study area is a montane and temperate forest. We took a location record, i.e. a GPS reading of

the study group's position, every 30 min or when we found fresh scat. Instead of doing conventional group follows for five consecutive days per month, we trailed the group whenever conditions were favorable and obtained an average of 82 location records per month. The usual 5-d-per-month sampling regime would have resulted in a drastic underrepresentation of the monthly home ranges because the group covers vast areas over the course of a whole month.

GPS readings for group location were entered into ArcView®. Total home range size was obtained by adding up the areas of all grid cells visited by the study group. The size of a grid cell is 0.0625 km^2, i.e. 250 x 250 m. Lacunae, i.e. cells not entered by the study group but surrounded by entered cells, were eliminated provided they contain supposedly suitable habitat (in our case all kinds of forest as opposed to open land), and isolated grid cells were linked with the minimum number of intervening cells containing suitable habitat. Three grid cells known to be pastures (unsuitable habitat) were not included in the computation of the home range size even they were surrounded by grids having been visited by the focal group.

For the calculation of seasonal and monthly home ranges, we applied a combination of the 100%-MCP method (MCP estimates based on all the fixes collected) and the grid cell method. We first created monthly and seasonal polygons ('unadjusted polygons') and then adjusted them by clipping out grid cells containing unsuitable habitat and grid cells that had never been visited. Unvisited grid cells became visible after overlaying the seasonal and monthly polygons with the total grid cell-based home range map. All ever visited grid cells fell into forested areas (based on a GIS vegetation strata map and ground truthing).

Results

Monthly range sizes varied enormously, depending on the method applied, e.g. the June range was 16.96 km^2 based on the uncorrected MCP and 14.52 km^2 based on the adjusted MCP; the grid cell approach, however, only yielded an estimate of 1.06 km^2 (Tab. 6.1). The MCP obtained value is 16 times larger than the grid based value. Original MCP consistently yielded the largest estimates of monthly and seasonal home ranges while the grid cell method yielded the most conservative ones. The adjusted polygon method yielded intermediate results (Tab. 6.1; Fig. 6.1). Furthermore, the total home range size estimate increased with increasing grid size. Using a 250 m grid, the home range size was 24.75 km^2, using a 500 m grid, it was 34.25 km^2.

Tab. 6.1. Monthly home range size estimates (in km^2) for the Gehuaqing group of *R. bieti* based on different methodologies.

Month	No. location records	Original MCP	Adjusted MCP	250 m grid	Relative difference between grid and MCP
200509	55	5.44	5.13	0.94	5.79
200510	107	1.27	1.27	1.25	1.02
200511	76	7.86	7.36	1.06	7.41
200512	90	5.96	5.83	1.88	3.17
200601	40	0.85	0.73	0.5	1.7
200602	42	9.94	5.13	1.31	7.59
200603	120	11.39	8.95	3.0	3.80
200604	124	19.52	12.77	4.06	4.81
200605	89	1.75	1.75	1.0	1.75
200606	53	16.96	14.52	1.06	16.00
200607	83	6.03	6.03	1.56	3.86
200608	103	15.60	10.48	2.44	6.39

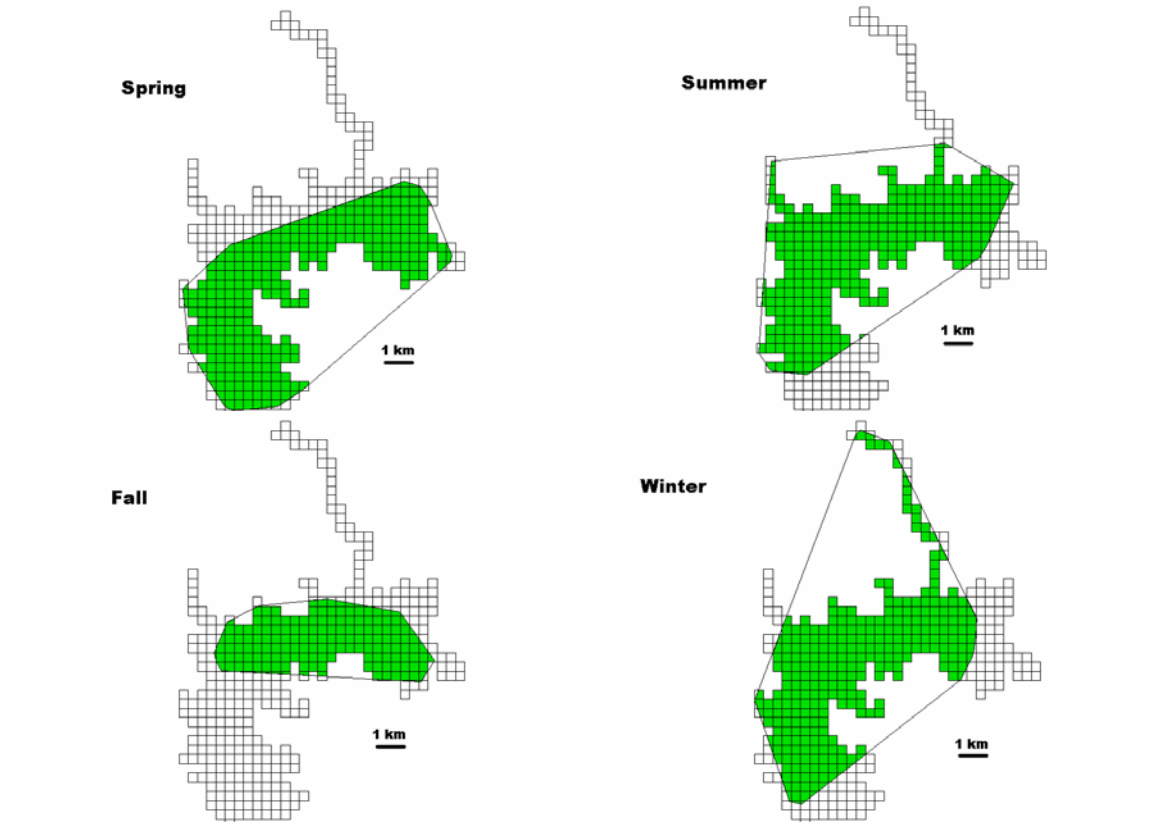


Fig. 6.1. Construction of adjusted polygons for seasonal home ranges of the Gehuaqing group of *R. bieti*: 'Unadjusted polygons' for each season were overlaid with the total grid cell-based home range map. Polygons were then adjusted by clipping out unvisited grid cells. For more details, see Methods.

Discussion

It is an established fact that the same data analyzed by different methods may yield highly variable numerical range size estimates [Macdonald et al. 1980]. This is in line with our findings. Thus choice of an inappropriate method may lead to the mischaracterization of a species' spacing system [Ostro et al. 1999], and this may have far-reaching consequences if such estimates of home range are used for drafting management concepts and for comparative socioecological analyses.

The grid cell method is highly affected by sampling intensity, and may only be the method of choice if laborious continuous group follows over a long time period are feasible. Otherwise application of the grid cell method results in an underestimation in monthly and (to

a lesser degree seasonal) home range size estimates because visits of the group to many grid cells within the home range will go undetected.

Compared to grid cell, the MCP method gives a far better approximation of monthly and seasonal home ranges in snub-nosed monkey studies. The MCP eradicates the problem of grid cells within the home range that are not visited and is more precise when the number of data points/location records is low [Robbins and McNeilage 2003]. Uncorrected MCP however yields far too large and hence unrealistic estimates because of peripheral data points. This disadvantage can be reduced by creating adjusted monthly and seasonal polygons, i.e. clipping out unsuitable habitat and areas never visited (cf. [Li and Rogers 2005; Mills and Gorman 1987]). The adjusted polygon method generates the most precise results. Instead of removing unused/unsuitable areas from the 100%-MCP, a 95%-MCP, whereby a certain proportion of the outermost locations are exluded [Worton 1995], is another way of mitigating the effects of outliers. However, these lack any biological basis [White and Garrott 1990]. Our method, though, is more precise and biologically meaningful since not a random area was deleted from the polygon, but an area known to constitute unused or unsuitable habitat.

Another issue that needs to be taken into consideration when employing the grid cell method is the selection of an appropriate cell size. White and Garrott [1990, p. 168] state that ”the coice of grid cell size is an arbitrary decision for which no biologically based, objective procedures are known”. However, one of the main assumptions underlying the choice of grid size is that it should be related to the typical spread of the group (as measured in two dimensions) (e.g. [Olson 1986; Ostro et al. 1999]. Moreover, the decision of setting a grid cell size shall be based on the average (or median) distance between consecutive locations [White and Garrott 1990], and - in case of application of GPS - also take into consideration satellite reception and associated positional accuracy of location records. We chose a 250-m grid because we found the usual spread of the band to be around 200 m.

It is beyond the scope of this methodological discourse to examine other relatively complex techniques such as Fourier series and fractal estimators in more detail (for more exhaustive reviews, see e.g. [Harris et al. 1990; Kernohan et al. 2001; Powell 2000; Sterling et al. 2000; White and Garrott 1990]). Recently, Kernel methods have become increasingly widespread in primate/animal ecology and are considered rather powerful (given that some underlying assumption such as independence of locational observations are met), e.g. [Izumiyama et al. 2003; Fashing et al. 2007b]. We did not use Kernels and therefore cannot

offer a quantitative assessment of the two methods. The kernel method provides an estimate for the utilization distribution, i.e. a probability density function that estimates an individual's or group's relative use of space. It shows the probability of locating an animal at a particular location on a plane [Worton 1989]. Compared to the traditional MCP which only uses information about home range borders and assumes a uniform probability distribution, Kernels give a more detailed and useful estimate of home range use and should be considered as alternatives to grid cell, MCP and adjusted polygons in future studies of snub-nosed monkeys. The here presented adjusted polygons provide a rather simple method that reliably computes monthly and seasonal home ranges of primates having large home ranges such as snub-nosed monkeys. This method is also preferable when sampling effort is irregular, an inherent problem associated with difficult-to-track snub-nosed monkeys. However, adjusted polygons require the incorporation of data on distribution of vegetation communities (suitable vs. unsuitable habitat) based on which the home range analysis can be fine-tuned.

CHAPTER 7 - Fallback Foods of Temperate-living Primates: A Case Study on *Rhinopithecus bieti*

Introduction

Various strategies exist in primates to deal with times of resource scarcity. Among the adaptations are: seasonal movements, seasonal breeding, altitudinal migration, nomadism, hibernation and dietary switching (reviewed in [van Schaik et al. 1993]; see also [Brockman and van Schaik 2005]). The phenomenon of fallback foods (foods that are relied upon when preferred items are unavailable (e.g. [Altmann 1974; Marshall and Wrangham 2007]) has been particularly well studied in the tropical great apes whose fallback foods include leaves, pith, THV (terrestrial herbaceous vegetation), bark, insects and figs [Knott 2005]. Other tropical primate taxa resort to palm nuts (*Cebus apella* [Struhsaker and Leland 1977]) or nectar (*Saguinus fuscicollis* [Terborgh and Goldizen 1985]).

Seasonal resource shortage characterizes primate populations in both the tropics and in the temperate zone, but the duration and harshness of the period during which fallback foods are essential may differ between them. Temperate habitats are characterized by relatively lower productivity and diversity [Cramer et al. 1999; Latham and Ricklefs 1993]. Temperate biomes thus impose different challenges on the primate consumer and entail specialized dietary adaptations.

The term 'temperate primates' refers to species that share the zoogeographic peculiarity of living mainly or exclusively within the temperate zone. The northern-hemisphere temperate zone extends from the Tropic of Cancer (at 23.5 degrees north geographical latitude) to the Arctic Circle (at 66.5 degrees north latitude.) The southern-hemisphere temperate zone extends from the Tropic of Capricorn (at 23.5 degrees south latitude) to the Antarctic Circle (at 66.5 degrees south latitude). In a nutshell, the main difficulties associated with inhabiting the northern temperate zone include "…the lower biological productivity of the land, the greater seasonality and reduced vegetation season, the great extremes in temperature, and the greater expenditures of energy required to maintain

homeostasis and reproduce" [Geist 1978, p. 271]. Only a small number of extant primate species are temperate-dwelling, e.g. the Chinese snub-nosed monkeys (*Rhinopithecus* spp.) and Japanese macaques (*Macaca fuscata*) are typical representatives of the North temperate zone and chacma baboons (*Papio hamadryas ursinus*) are inhabitants of the South temperate zone. Some local environments inhabited by North-temperate species are extreme by primate standards, with lowest recorded temperatures of -30° C (*Rhinopithecus roxellana* [Su et al. 1998]), -25° C (*R. bieti* [Li et al. 1982]), -20° C (*Macaca mulatta* [Qu et al. 1993]), and -19.5 °C (*M. fuscata* [Suzuki 1965]). However, even within the temperate zone, there are habitats that are warmer and more subtropical in nature; this applies especially to lower lying habitats in areas with strong vertical vegetative zonation, e.g. Samage in China [Li et al. 2008] and Yakushima in Japan [Hanya et al. 2003].

Black-and-white snub-nosed monkeys (*Rhinopithecus bieti*), alternatively referred to as Yunnan snub-nosed monkeys, are among the few non-human primates able to cope with hostile environmental conditions associated with living in cold temperate montane forests. These heavy, stocky primates of the subfamily Colobinae are highly endangered (total population size <2000) and have an extremely restricted geographic distribution in the Hengduan Mountains which border the Himalaya Range (Long et al. 1994). They primarily inhabit temperate alpine forest ecosystems and occasionally venture into incredibly high elevations, reaching 4'700 m [Long et al. 1996]. Yunnan snub-nosed monkeys live in very large super-groups or bands which are composed of single-male core families or harems [Kirkpatrick et al. 1998; Chapter 3 in this thesis]. They move as cohesive groups inside vast non-defended home ranges [Kirkpatrick et al. 1998; Chapter 5 in this thesis].

Pronounced seasonality in their climatologically extreme natural habitat produces temporal fluctuations in plant food availability and a prolonged winter season characterized by scarcity of edible plant resources. Unlike many tropical-living primates which have the option of turning to young leaves in times of fruit shortage [van Schaik and Brockman 2005], the temperate-living snub-nosed monkeys face a lean season for both fruit and flush at the same time and experience seasonally pronounced dietary stress. The vegetation at the study site (Samage) is dominated by evergreen trees such as conifers, oaks and azaleas (Chapter 8 in this thesis) whose foliage is known for low palatability [Kirkpatrick 1996]. All deciduous trees are bare by early winter, and this natural abscission further enhances the severity of the 'dietary dilemma' confronting the monkeys. In this chapter, I elucidate how this cumulative absence of palatable plant parts in winter is dealt with by the snub-nosed monkeys and how

they allocate their feeding time to various food items throughout the annual cycle in relation to plant phenology. I compare the results obtained at two different sites showing different levels of productivity. I discuss possible implications of their fallback strategy on various aspects of their biology, including range use, sociality, masticatory morphology, and conservation. I also put our findings within a comparative context by offering a preliminary review of fallback strategies in other temperate primates.

Methods

Study Location

I conducted the present study in the predominantly temperate Samage Forest (27°34'N, 99°17'E) in Yunnan's Baimaxueshan National Nature Reserve. Narrow valleys and steep hillsides characterize the topography at Samage. Land cover at the research area is a mosaic of various vegetation types. Along an ascending altitudinal gradient, the forest grades from evergreen broadleaf forest at 2'500-3'000 m (mostly subtropical oaks of the genus *Cyclobalanopsis*) and *Pinus yunnanensis* forest at 2'500-3'100 m forest to predominantly mixed coniferous and deciduous-broadleaf forest at 2'900-3'600 m to mostly *Abies georgei* forest at 3'500-4'000 m. Parts of the Samage Forest have been selectively logged, and herdsmen let cattle graze on spacious alpine meadows in the summer. Collection of mushrooms and herbal plants by villagers is widespread.

The snub-nosed monkeys' habitat at this locality ranges from 2'500 m to 4'000 m and includes all major vegetation types, with the monkeys showing a strong preference for mixed forest and avoidance of clearcuts [Chapter 4 in this thesis]. The focal group is composed of at least 410 members. For more details on the study site and study group, see [Chapters 4 and 5 in this thesis].

The climate data presented here are based on two years while the data in Chapter 4 are based on 1 year. Climate data were gathered at an altitude of 2'448 m (800 m below the most frequently used altitude of the study group). Mean annual rainfall was 1'004 mm (mean of two measurements with two different rain gauges). Distribution of precipitation was highly irregular. The highest monthly rainfall was 275 mm in August 2007, the lowest 0 mm in January 2006 and January 2007 (Fig. 7.1). There was a steep increase in rainfall from spring onwards and a prolonged dry season with minimal precipitation from November to February

(in both years) and high irradiance during which the vegetation became desiccated. Most snowfall occurred in February (in both years) during which snow accumulated up to 80 cm in depth at an elevation of 3100 m. Higher areas were temporarily off limits due to even greater snow depth.

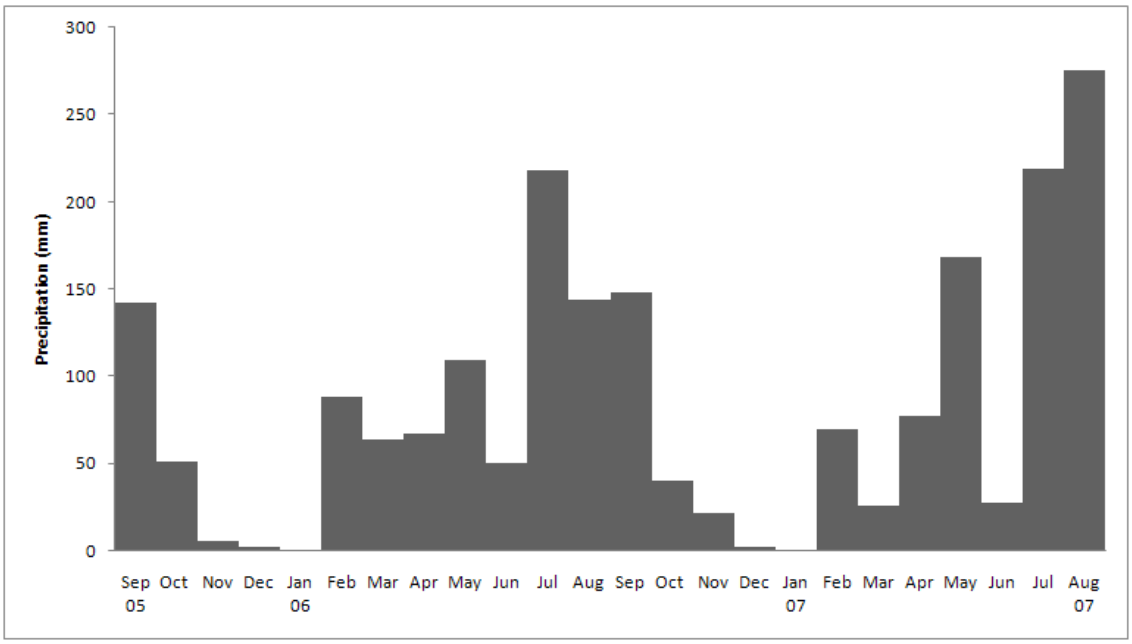


Fig. 7.1. Monthly precipitation [mm] in the Samage Forest from September 2005 to August 2007. Precipitation in February was mainly in the form of snow.

Mean annual temperature was 14.3 °C. Temperature varied strikingly with seasons: Temperatures fell between two extremes of -3.8°C in January 2007 and 35.4°C in July 2006. The two winters covered during this study were relatively mild compared to previous winters and the subsequent one, e.g. the lowest recorded temperature in winter 2007/08 was -7.9 °C. The month with the highest average temperature was July 2006 (21.5°C), the month with the lowest average temperature was January 2007 (6.6°C) (Fig. 7.2). There were considerable day-night fluctuations in temperature, especially in winter. Greatest daily temperature range was 26.4°C. For more details on the area's climate, see Chapter 4 in this thesis.

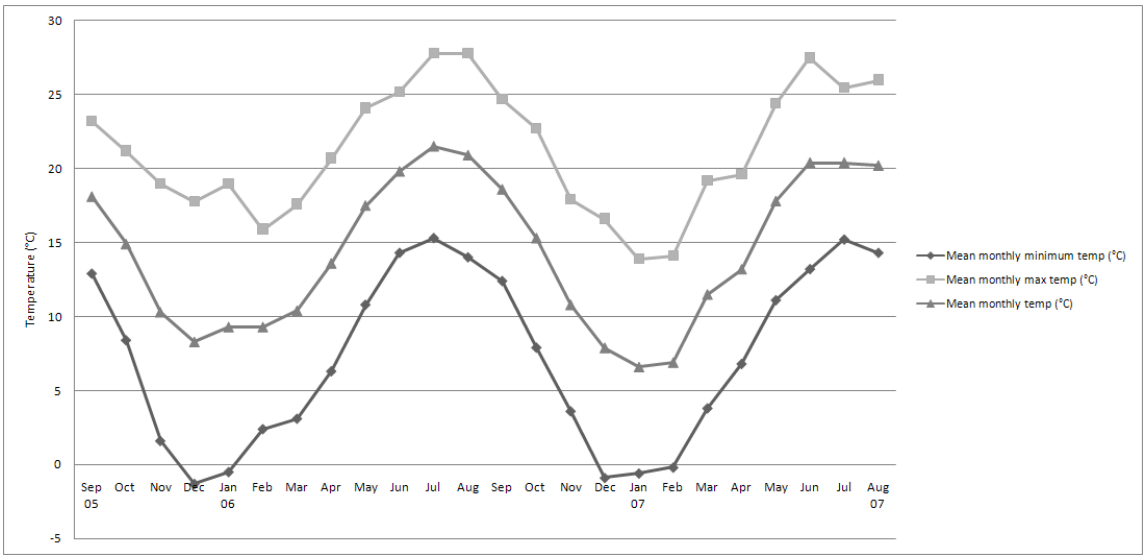


Fig. 7.2. Mean monthly temperature and mean monthly minimum and maximum temperatures in the Samage Forest from September 2005 to August 2007.

Data Collection

Feeding Observations

We established contact with the focal group on an average of 12 days per month throughout the 20-month study period (Sep 2005 – May 2006; Aug 2006 – Nov 2006; Jan 2007 – Jul 2007). We usually located the group based upon its position during previous observation days and information about the animals' whereabouts gained from local rangers. Using a high-performance spotting scope (Kowa® TSN 820, 20-60x Zoom), behavioral observations were usually conducted from rocky outcrops, ridges or hillsides at a distance of 50-1'200 m to the location of the monkey group. These *distance observations* (>100 m) ensured that the group was not perturbed and allowed us to obtain a better overview of the spatial configuration of the group members and see into forest patches that were difficult to reach on foot. However, group members now and then accepted the main researcher (CCG) to stay within 10-30 m (flight distance) to them (*close observations*, <100 m).

Systematic data on diet were collected via scan sampling [Altmann 1974; Morrison et al. 1998] of the focal group. Scans of all visible animals were taken at 15 min or 30 min intervals ($n_{15\text{-min scans}}$ = 1'372, $n_{30\text{-min scans}}$ = 225) (Tab. 7.1.). The decision of choosing 15 vs. 30 min intervals depended on the number of animals in view. If a large number of monkeys

was in view, 30-min scans were made; if only a small fraction was visible, 15-min scans. As a rule of thumb, intervals were usually 15 min during close observations and 30 min during distance observations, but not exclusively. The main criterion for choosing a scan interval was that a scan had to be completed at least 5 min before the beginning of the next scan. Every scan included information on date and time and weather conditions. For every subject being scanned, I recorded age, sex, activity, and distance to nearest neighbor. The individual was recorded as 'unknown' if age/sex class could not be recognized due to low visibility or only some fur or tail parts being visible.

Tab. 7.1. No. of scans for every month.

Month-year	No. of scans	No. of 15-min scans	No. of 30-min scans
Sep-05	60	40	20
Oct-05	141	134	7
Nov-05	75	61	14
Dec-05	83	51	32
Jan-06	27	26	1
Feb-06	19	6	13
Mar-06	115	93	22
Apr-06	98	90	8
May-06	78	70	8
Jun-06	0	0	0
Jul-06	0	0	0
Aug-06	61	58	3
Sep-06	107	89	18
Oct-06	89	87	2
Nov-06	93	65	28
Dec-06	0	0	0
Jan-07	74	56	18
Feb-07	56	46	10
Mar-07	62	61	1
Apr-07	125	124	1
May-07	64	55	9
Jun-07	84	79	5
Jul-07	86	81	5
Total	1597	1372	225

Group members were often spread out over large distances (>100m) in the forest and across forest strata, precluding data collection on all members of the group during a single scan. Because animals on the ground were frequently overlooked during scans due to poor visibility, there is some bias towards feeding on arboreal food items. I occasionally changed our location between scans to sample different portions of the group. Sampling was

discontinued during periods of heavy rain/snow and dense fog. I strove to get scan data from mornings, evenings, and afternoons.

Activities were grouped into mutually exclusive categories, following the definitions in the Appendix to Chapter 3 in this thesis. *Feeding* is the only activity of importance here and is defined as inspecting and picking food with hand or mouth, manipulating food, putting food into the mouth, and chewing. While feeding does not include inactivity during feeding sessions, it includes obvious search for food.

Observation conditions permitting, scan records of feeding behavior also included the food item, plant part and its age as well as plant species. The following foods were distinguished: lichens (fruticose vs. foliose), young leaves (including spring buds/shoots), mature leaves, buds (dormant leaf and flower buds), flowers, bark, pith, herbs, fruit (both ripe and unripe), invertebrates, snow, fungi, water, bamboo shoots, and tuber. Flower buds were often hard to distinguish from leaf buds when observing via telescope, so I included them in 'buds'. It was difficult to see whether the small fruits were eaten wholly or whether the flesh was discarded, so I did not distinguish between seeds and pulp/rind. Moreover, both leaf blades and petioles were treated as 'leaves'. Limited visibility made it difficult to consistently recognize the item ingested, and for the following analyses feeding records lacking information on the nature of the food item were omitted. For analyses, the following categories were lumped into 'other': bark, snow, tuber, water, fungi, and invertebrates. I also recorded whether the animals fed in a broadleaf, conifer or dead tree and noted the tree species and genus whenever possible.

There were some potential biases associated with collecting dietary data via scan sampling: as a result of differential visibility of animals in the canopy and on the ground, the proportion of the diet devoted to arboreal items such as lichen is likely to be overestimated in relation to terrestrial foods such as THV (cf. [Isabirye-Basuta 1989]). Moreover, conifer trees usually tower above a mid-layer of deciduous trees which may be cause fruit/leaf eating to be underrepresented compared to lichen eating because fruits/leaves are found mostly in deciduous trees and lichens are most often associated with conifer trees.

During forest walks outside the scan sessions, I recorded all partially consumed and discarded foods on the forest floor with tooth marks or other signs of having been handled. I used evidence from such feeding sign as a complementary measure to estimate seasonal variance in diet composition, and used their diameter to roughly divide them into large, small and medium sized ones to allow for quantification.

Tree and Lichen Survey

Using a stratified random sampling design [Mueller-Dombois and Ellenberg 1974] and taking into account the proportional availability of distinct habitat types as well as altitudinal stratification, we established a total of 67 plots of 20 m x 20 m each. For details on plot design, see Chapter 4 in this thesis. We recorded various physical dimensions for all trees (girth >40 cm) in the plots [Chapter 4 in this thesis] and identified individual trees (n = 1'851) to species or genus level using reference books [Raven and Wu 1994-2005; Unknown 1972] and via collection of vouchers.

Each of the marked trees was given a lichen-load category, ranging from 0 for 'None' to 4 for 'Heavy', following [Kirkpatrick 1996] and [MacLennan 1999] and representing a simple and effective method of evaluating the biomass of arboreal lichens available to snub-nosed monkeys as potential forage.

To estimate the regeneration time of lichen, a one-year growth experiment was conducted. Fifteen trees (oaks and conifers) within the core zone of the group's home range were selected. In each tree, one live branch over 10 cm in circumference was designated, and circumference was recorded. All fruticose lichens were then stripped from these branches. After one year we stripped all lichens from the same branches and dried them to constant weight. Lichen growth, i.e. replacement rate (percent per year) was calculated by dividing the weight of lichen collected from the 'stripped' stem at year's end by the weight collected at the year's beginning [Kirkpatrick 1996].

Of the 1'851 enumerated trees, 307 trees were selected for monthly phenological monitoring, and another subset of 157 deciduous monoecious trees from 21 genera known to contribute significantly to the diet (Chapter 8 in this thesis) was then selected for the analyses presented in this chapter. These latter phenological records were intended to characterize seasonal changes in the availability of *R. bieti* food resources. Trees chosen for phenological monitoring were mature individuals with girth over 40 cm that offered a good view of their crowns. We conducted phenological sampling at monthly intervals between the 6th and 13th of each month, when we visually inspected each marked tree, and recorded the presence of fruits and open flowers (reproductive parts) as well as young leaves and senescent leaves (vegetative parts). Mature and immature fruits were noted simply as fruits due to difficulties in determining the maturity of many fruits based on a visual assessment through binoculars.

Temporal availability of bamboo shoots (*Fargesia* cf. *melanostachys*) was investigated in five specifically designed bamboo plots (two at 3'650 m and three at 3'400 m)

by recording the density of bamboo culms vs. shoots at monthly intervals in spring and summer (April to July 2007). Young shoots were easily identifiable from older stems/culms based on softness, color, and height.

Data Analysis

The behavior of every animal scanned was intended to be an instantaneous sample. The practice of alternating between 15- and 30-min scan intervals yielded two data sets (DS15 and DS30). I compared the two data sets and found significant differences in proportional representation of both major age/sex classes (χ^2 = 9.78, df = 3, p = 0.021) and specific food items (χ^2= 59.4, df = 4, p < 0.001). I therefore analyzed the two data sets separately. Proportions of the different food items in the diet were calculated for each month and each season.

For the main phenological analyses, I calculated the proportion of monitored trees bearing each of the phenophases every month (presence vs. absence). For the analysis of leaf senescense (as evidenced by obvious changes in color), deciduous angiosperm trees were ranked on a scale reflecting percent of senescent leaves out of all present leaves (*0* = 0%, *2.5* = <5%, *15* = <25%, *37.5* = <50%, *87.5* = <75%, *100* = 100%). The period of leaffall was monitored by noting whether a tree was bare, had full foliage or was partly defoliated. For the analysis of bamboo shoot availability, the number of shoots/the number of culms x 100 (% of ground shoots) was used to estimate monthly availability of shoots relative to the availability of culms in the forest [Tan 2000].

Results

Phenological Patterns

Fruit production peaked in August, and the majority of species fruited at some stage during the rainy season or during the transition between the rainy and dry season (Fig. 7.3). Deciduous trees produced new leaves in big bursts, and this leaf flush coincided with the onset of the monsoon season, as evidenced by a positive correlation between rainfall and young leaf availability (r_s = 0.462, p = 0.026, *n* = 23). Deciduous leaves started becoming

senescent in October and were mainly shed in November and December (Fig. 7.4). All deciduous trees were bare by January as a result of this natural abscission. None of the phenophases showed a peak in availability in winter.

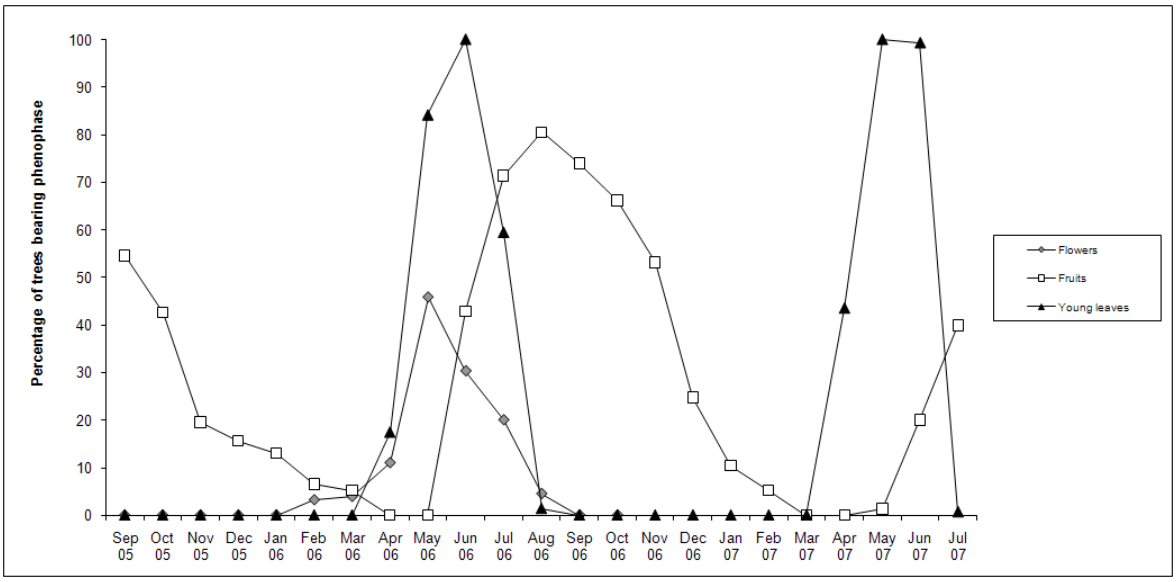


Fig. 7.3. Availability of fruits, young leaves, flowers of *R. bieti* food trees at the Samage Forest, in 2005/2006/2007. Data come from 157 sampled tree specimens.

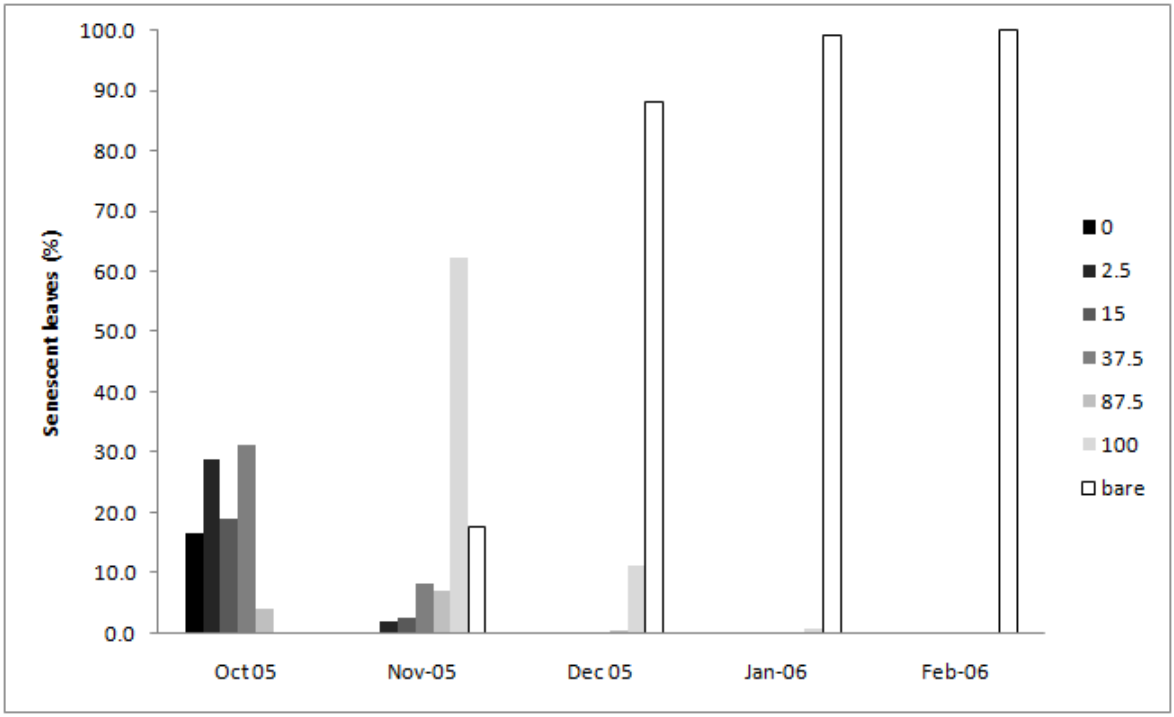


Fig. 7.4. Temporal patterns of leaf shedding of deciduous angiosperms at Samage. The numbers denote the percentage of senescent leaves. For details, see text.

Seasonality in Food Use

The results are founded on a total of 2'674 feeding records (1'784 in DS15, 890 in DS30) that included information on the identity of the ingested food item. By averaging monthly proportional representations of particular food items, I obtained an annual percentage for each food type (the first number refers to DS1, the second to DS2: lichens 66.0/67.7%, fruits 13.9/8.8%, young leaves 12.9/11.9%, mature leaves 4.0/4.2%, buds 2.3/4.8%, flowers 0.2/0.1%, herbs 0.3/2.0%, other 0.5/0.5%.

The relative representation of food items in the diet varied widely among months (Tab. 7.2). Fruit consumption showed a sharp peak in August. Utilization of lichens dropped precipitously as new foliage became available in spring. Amount of young leaves in the diet correlates with phenological availability (DS15: $r_s = 0.863$, $p > 0.001$, $n = 20$; DS30: $r_s = 0.867$, $p > 0.001$, $n = 19$; Fig. 7.5). The amount of fruit in the diet also showed a positive correlation with availability (DS15: $r_s = 0.636$, $p = 0.003$, $n = 20$; DS30: $r_s = 0.714$, $p = 0.001$, $n = 19$). The proportion of flowers in the diet correlates with availability in DS15 ($r_s = 0.725$, $p = 0.008$, $n = 12$), but not DS30 ($r_s = 0.218$, $p = 0.519$, $n = 11$). Flowers were available only during a short temporal window in spring during which they were consumed occasionally. Overall, they did not form a noticeable portion of the monkeys' diet.

Tab. 7.2. Monthly variation in the percent of feeding records as a function of food type. (a) DS15, (b) DS30.

(a)

Month	*n*	Lichens	Buds	Fruits	Mature leaves	Young leaves	Flowers	Herbs	Other
Sep 05	32	62.5	3.13	34.38	0	0	0	0	0
Oct 05	151	80.79	0	3.31	14.57	0	0	0	1.32
Nov 05	99	98.99	1.01	0	0	0	0	0	0
Dec 05	93	96.77	3.23	0	0	0	0	0	0
Jan 06	38	100	0	0	0	0	0	0	0
Feb 06	16	93.75	0	0	0	0	0	0	6.25
Mar 06	137	89.78	8.03	0	2.19	0	0	0	0
Apr 06	203	36.45	0	0	2.46	60.1	0.49	0.49	0
May 06	157	20.38	0.64	0	0	71.34	7.64	0	0
Aug 06	134	27.61	0	66.42	5.22	0	0	0.75	0
Sep 06	159	60.38	0	32.7	6.92	0	0	0	0
Oct 06	98	51.02	0	25.51	19.39	0	0	0	4.08
Nov 06	165	62.42	0	26.06	11.52	0	0	0	0
Jan 07	145	80.69	8.28	10.34	0.69	0	0	0	0
Feb 07	122	86.89	10.66	0.82	0.82	0	0	0.82	0
Mar 07	102	90.2	4.9	4.9	0	0	0	0	0
Apr 07	276	40.94	0	0	0.72	53.98	2.54	1.45	0.36
May 07	149	44.97	0	0	0	55.04	0	0	0
Jun 07	181	54.7	0	0	0	45.3	0	0	0
Jul 07	160	95.63	0	0	2.5	0	0	0	1.88

(b)

Month	*n*	Lichens	Buds	Fruits	Mature leaves	Young leaves	Flowers	Herbs	Other
Sep 05	34	79.41	0	11.76	8.82	0	0	0	0
Oct 05	24	83.33	0	4.17	12.5	0	0	0	0
Nov 05	104	94.23	0.96	0	4.81	0	0	0	0
Dec 05	102	98.04	0	0	1.96	0	0	0	0
Jan 06	9	100	0	0	0	0	0	0	0
Feb 06	29	93.1	0	0	6.9	0	0	0	0
Mar 06	101	84.16	3.96	0	7.92	0	0.99	0	2.97
Apr 06	48	62.5	0	0	0	37.5	0	0	0
May 06	40	7.5	0	0	0	92.5	0	0	0
Aug 06	23	65.22	0	26.09	8.7	0	0	0	0
Sep 06	108	55.56	0	31.48	12.04	0	0	0	0.93
Oct 06	0								
Nov 06	177	59.32	0	29.94	10.73	0	0	0	0
Jan 07	156	50	12.82	14.1	0	0	0	23.08	0
Feb 07	62	85.48	11.29	0	0	0	0	0	3.22
Mar 07	9	66.67	33.33	0	0	0	0	0	0
Apr 07	17	29.41	0	0	0	70.59	0	0	0
May 07	75	41.33	0	0	1.33	53.33	1.33	1.33	1.33
Jun 07	32	81.25	0	0	0	18.75	0	0	0
Jul 07	105	97.14	0	0	2.86	0	0	0	0

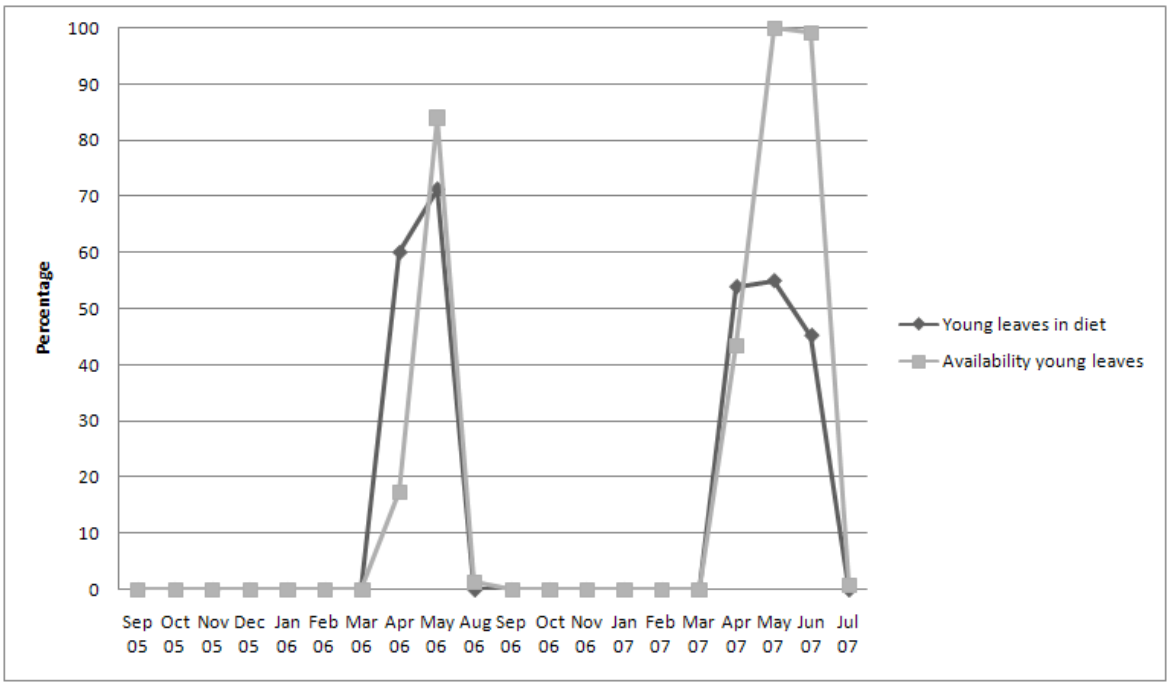
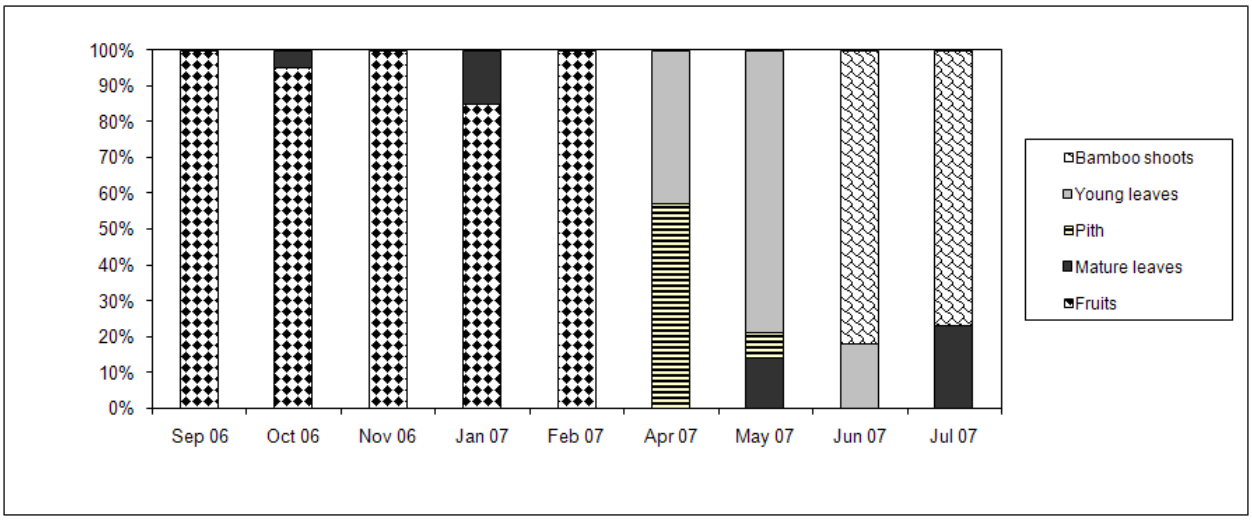
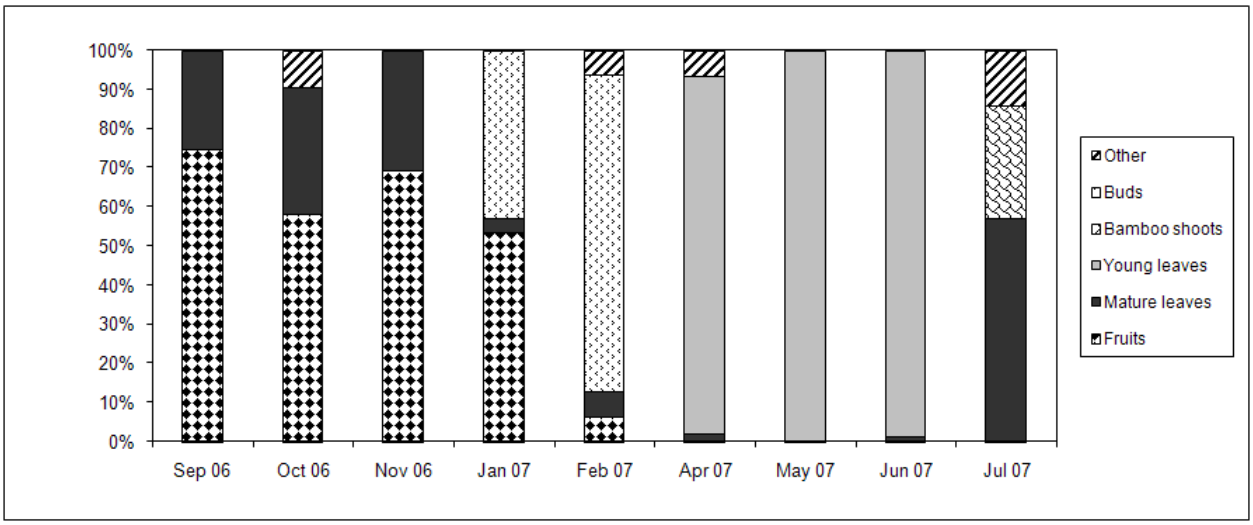


Fig. 7.5. Comparison of how young leaf consumption varies with young leaf availability. 'Young leaf in diet' refers to the percentage of feeding time on young leaves, 'availability of young leaves' refers to the percentage of trees bearing young leaves.

The first bamboo shoots appeared in May at mid-elevations. Bamboo shoot availability in plots (at high elevations) was 0 in April and May. The relative availability of bamboo shoots was 30.5% in June and 36.4 % in July. Based on inspections of feeding sign, bamboo shoots represent a key food in summer (Fig. 7.6a), but only a few instances of bamboo shoot consumption appear in the scan samples (Fig. 7.6b). So while the scan data imply that July is characterized by absence of nutritionally interesting plant foods and high reliance on lichen (96-97% of the feeding records), detritus found in the group's foraging path demonstrates that lichens are complemented with a substantial amount of bamboo shoots.



(a)



(b)

Fig. 7.6. (a) Monthly diet composition for a limited number of months during which feeding sign could be assessed. Lichen use could not be quantified since lichen is rarely found in feeding litter. (b) Monthly diet composition based on 15-min scans after excluding lichens. A comparison between the two methods reveals that bamboo shoots and also pith are much more prominent in the data set based on feeding sign.

Lichens: Representation in the Diet, Distribution and Regeneration

Lichens were consumed in every single month and ranked first in the diet in every month, except in April 2006 (DS15), May 2006 (both DS), April/May 2007 (both DS) when young leaves dominated the diet and August 2006 (DS15) when fruits predominated. Both use of young leaves and availability of young leaves were negatively correlated with percentage of lichen feeding records (Tab. 7.3). There was neither a correlative association

between use of lichen and use of fruit nor between use of lichen and availability of fruit. I compared the percentage of time invested in lichen vs. non-lichen feeding between males and females and found for DS15 that males spent significantly more time feeding on lichens than females (χ^2 = 4.668, df = 1, p = 0.018). However, as for DS30, there was no significant difference between males and females (χ^2 = 0.100, df = 1, p = 0.409).

Tab. 7.3. Correlation matrix comparing feeding records for lichens with feeding records for plant parts and availability of plant parts.

	Availability						Representation in diet			
	Fruit		Young leaves		Fruit and/or young leaf		Fruit		Young leaves	
Representation of lichen in diet	DS1	DS2	DS1	DS2	DS1	DS2	DS1	DS2	DS1	DS2
	0.044	0.252	-0.658**	-0.490*	-0.681**	-0.499*	-0.249	-0.349	-0.668**	-0.616**

The following lichen species were implicated as food by the snub-nosed monkeys at Samage: *Usnea longissima*, *Usnea* sp., *Bryoria confusa*, *Bryoria* cf. *trichodes* cf. ssp. *americana*, *Cetrelia* sp. and 1 unknown species (all Parmeliaceae). Of all the picked lichens that could be identified, 90.1/91.0% were *Usnea* spp. (almost exclusively *U. longissima*; Fig. 7.7), 8.1/5.1% foliose and 1.8/3.9% *Bryoria* spp.

Fig. 7.7. Male *R. bieti* feeding on the lichen *Usnea longissima*. Adult males spent more time feeding on lichens than adult females. Photo © J. Weingarten.

I conducted some limited 'cafeteria-style' trial experiments with a captive subadult male from the local population that was temporarily held at the Samage Forest Research Station. In a first trial, approximately equal amounts of lichens *(Usnea longissima*) and *Sorbus* sp. fruits/leaves (one of the local monkeys' preferred plant food [Chapter 8 in this thesis]) were offered concurrently for 41 times, alternating the sides. In 39 cases, the animal chose lichens, in 2 cases *Sorbus*. In another trial experiment repeated 24 times, *Usnea* and *Bryoria* lichens were offered. In 19 cases the monkey chose *Usnea*, in 5 cases *Bryoria*. These preliminary results suggest preference for lichens over at least one plant food and preference for *Usnea* over *Bryoria* lichens.

Lichens were available year-round at the site. Seventy-six percent of the sampled trees were covered with lichens (including the mesophytic evergreen broadleaf trees). I tested for a relationship between DBH (diameter at breast height) and lichen load using all the trees except the trees in the mesophytic evergreen broadleaf forest since these have only scant lichen cover. Lichen cover is significantly positively related to DBH ($r_s = 0.312$, $p = 0.001$, $n = 1649$, one-tailed). Canopy volume and lichen load are positively correlated ($r_s = 0.107$, $p = 0.001$, $n = 1649$, one-tailed). So DBH can be seen as a proxy measure for lichen cover.

Lichen cover is clearly associated with elevation: the higher the elevation, the larger the lichen load (Fig. 7.8).

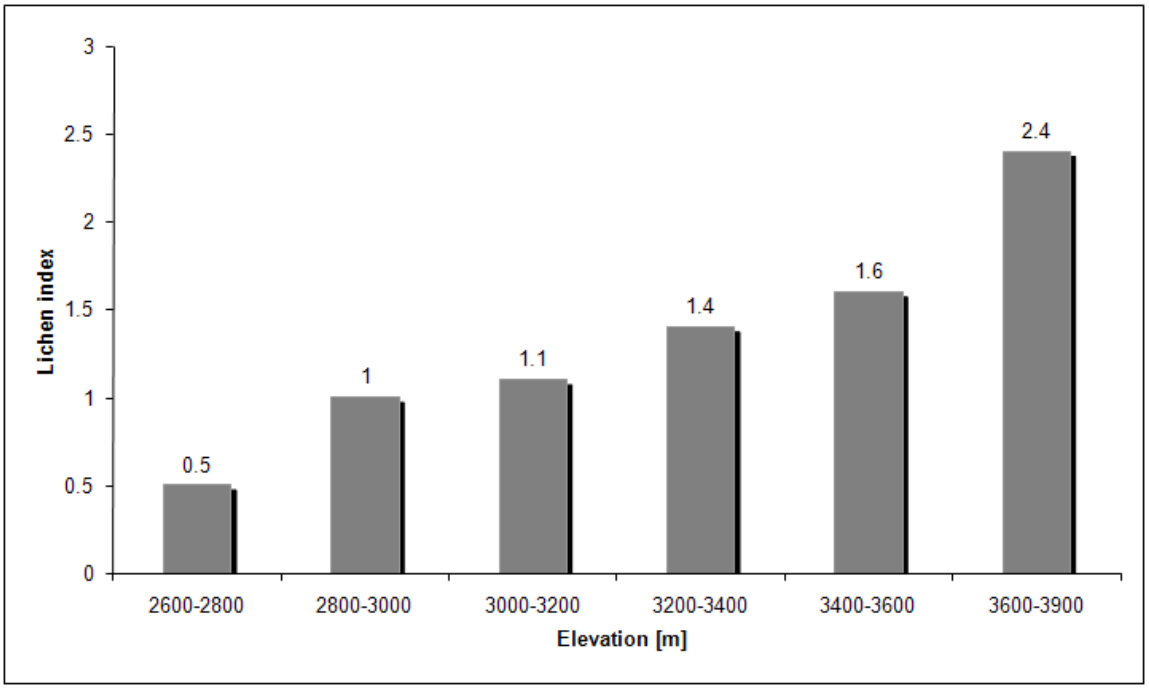


Fig. 7.8. Lichen index of 1'851 trees compared among altitudinal zones at the Samage Forest. For details on how the lichen index was obtained, refer to the text.

Different tree species varied with regard to lichen cover (Tab. 7.4). Sclerophyllous oaks (*Quercus pannosa*, *Q. rehderiana*) were most densely laden with lichens (2.1, standard deviation SD 0.8), followed by conifers (1.8, SD 1.0) and angiosperm trees (excluding sclerophyllous oaks) (0.9, SD 0.7). The differences in lichen load among all three categories are highly significant (ANOVA, $F_{2,\ 1894} = 341.4$, $p = 0.001$). Dead trees ($n = 40$) supported moderate lichen growth (1.3). The vast majority of lichen feeding was recorded in conifer trees, i.e. 80.1/75.7% conifers, 10.2/13.9% angiosperms, 6.7/7.1% oaks, 3.0/3.3% dead trees. The regeneration study revealed that lichens need an average of 21.4 years to regrow to the initial length ($n = 14$, after removing one outlier).

Tab. 7.4. Lichen load categories for various tree species in the Samage Forest, in descending order.

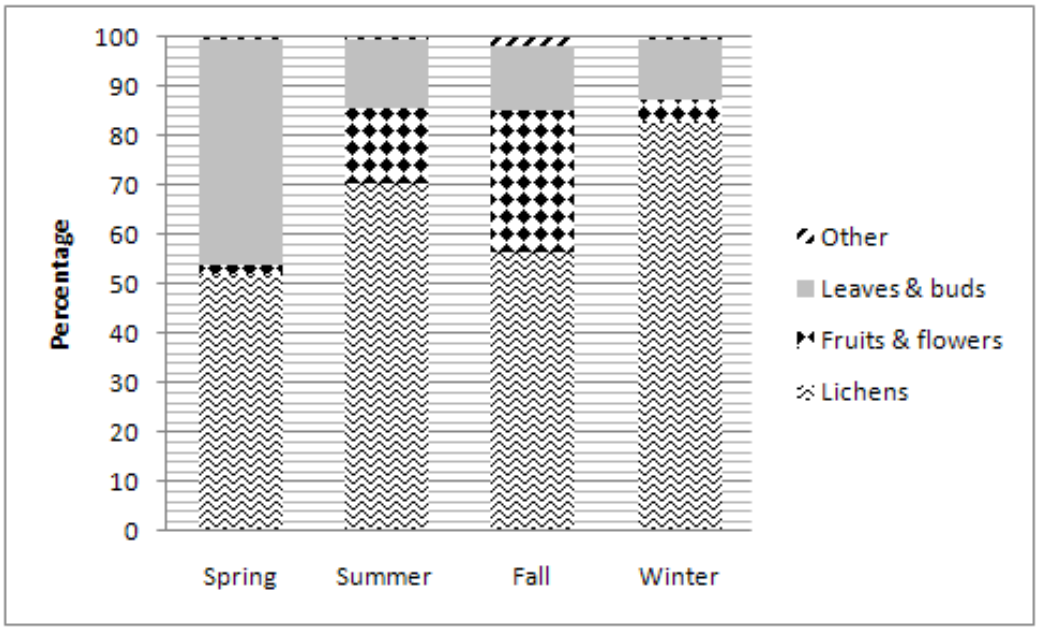
Species	Lichen index
Abies georgei (Pinaceae)	2.47
Quercus pannosa (Fagaceae)	2.46
Picea likiangensis (Pinaceae)	1.81
Pinus yunnanensis (Pinaceae)	1.39
Rhododendron rubiginosum (Ericaceae)	1.38
Tsuga dumosa (Pinaceae)	1.35
Quercus rehderiana (Fagaceae)	1.33
Abies ernestii (Pinaceae)	1.31
Rhododendron anthosphaerum (Ericaceae)	1.30
Salix rehderiana (Salicaceae)	1.28

Discussion

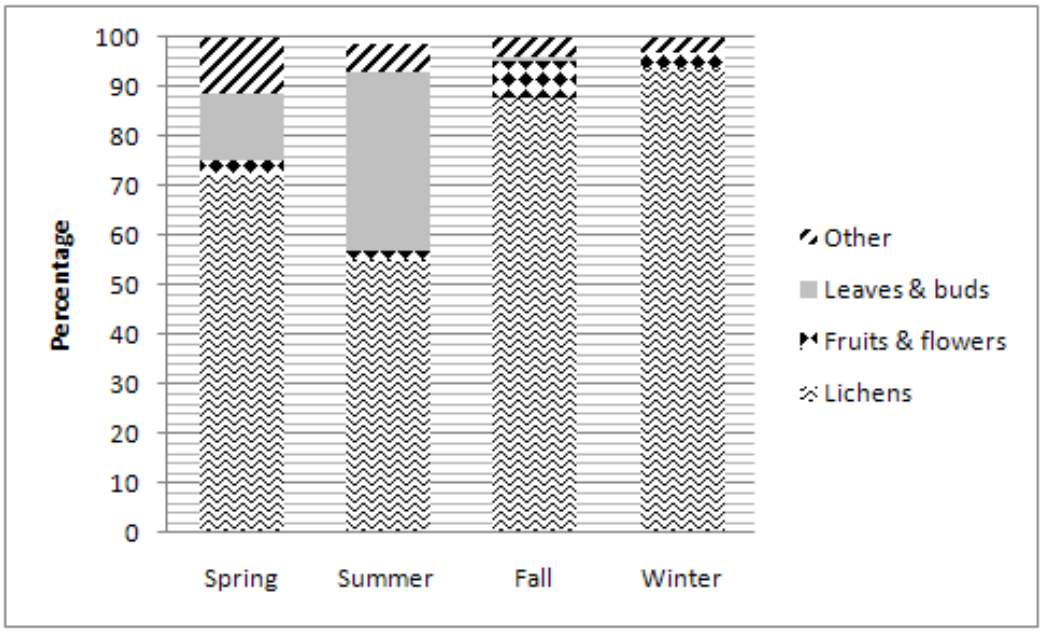
Dietary Strategy of *Rhinopithecus bieti* at Samage and a Comparison with Other Populations

Fallback foods have been operationally defined as foods whose use is negatively correlated with the availability of preferred foods (e.g. [Altmann 1998]). In line with Xiang et al. [2007a], my data confirm for the *R. bieti* group at Samage that there is a negative correlation between the proportion of lichen in the diet and the availability of young foliage. This inverse relationship indicates that lichens act as a fallback or backup food, and together with the high proportional representation of young leaves in the monkeys' diet during the spring flush, these results provide clear evidence that young foliage is a highly preferred dietary constituent. The results obtained from another study at Xiaochangdu (ca 200 km to the north of Samage) show an overall similar dietary pattern, but the lower productivity there (higher altitude and latitude, lower temperature and rainfall and tree species diversity) constrains foraging options and causes differences in a few respects (Fig. 7.9). First, at Xiaochangdu, lichens are slightly more important in terms of annual representation in the diet (75 vs. 67%) and basically constitute the only available winter food item. The effect of productivity on lichen use is corroborated by a positive association between altitudinal distribution and proportion of lichen in the diet of different populations (Fig. 7.10). Second, fruit plays a more important role in the diet of the monkeys at Samage. Third, young leaves become available

later at higher altitudes at Xiaochangdu and are thus part of the early summer diet and not late spring diet as at Samage.



(a)



(b)

Fig. 7.9. Seasonal diet composition in percent of the *R. bieti* group at Samage (a) compared with the group at Xiaochangdu (b). Data for Samage are based on the present study, data for Xiaochangdu are based on [Xiang et al. 2007a]. The value of 75% lichen feeding at Xiaochangdu represents a weighted mean of two different sampling methods, i.e. group follows and telescope observations; using only data obtained from telescope observations, lichens made up 82% of the total diet.

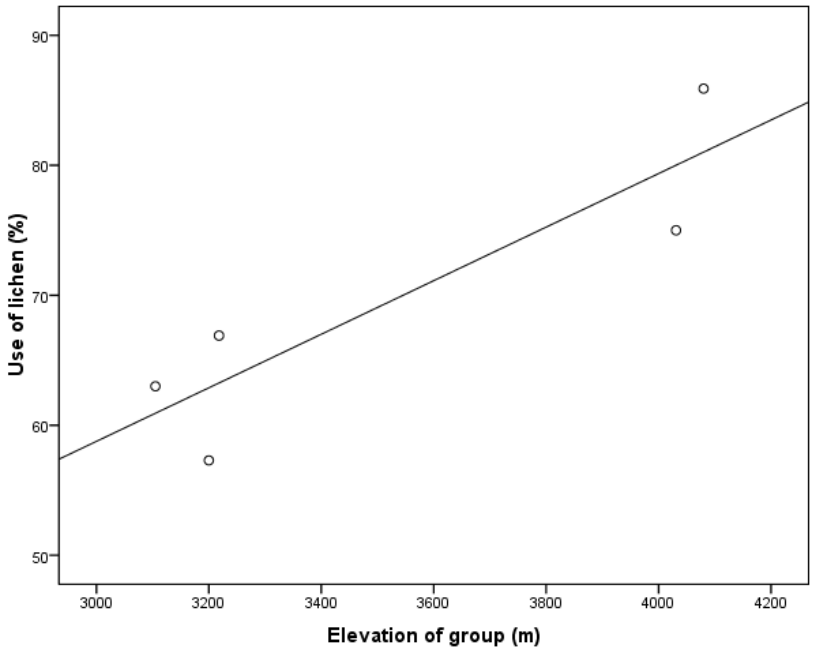


Fig. 7.10. Correlation between the importance of lichen in diet (percent feeding records) and mean elevation of different study groups of *R. bieti*. Data are based on [this study; Ding and Zhao 2004; Kirkpatrick 1996; Liu et al. 2004; Xiang et al. 2007a].

The percentage of feeding records is a proxy for the total time invested in feeding on a particular item and thus indicates the importance of a particular food [Marshall and Wrangham 2007]. Because lichen feeding accounted for ca 67% of the diet, lichens are evidently an essential food item. Marshall and Wrangham [2007] distinguished between two classes of fallback foods, staple and filler fallback foods. According to their definition, staple fallback foods are available perennially, are usually consumed throughout the year, seasonally can constitute up to 100% of diet, and are uniformly distributed. Filler fallback foods, on the other hand, never make up 100% of the diet, are completely avoided for some time (weeks, months), and are rather patchily distributed. Lichens are eaten in every month and season by *R. bieti* at Samage, albeit with varying percentages, and hence constitute a staple fallback food.

The significance of fruits in the diet reached a peak in late summer/early fall and decreased subsequently. Fruits such as *Sorbus* and *Acanthopanax* persist long into winter and survive frost periods. By feeding intensively on fruit in the fall, the animals can deposit fat which can be drawn upon during the severe winter (cf. [Hamada et al. 2003; Zhao 1994]). Fruits are, however, a somewhat unreliable resource. In the fall 2006, many rowan (*Sorbus* spp.) fruits suffered from fungus attacks which probably resulted in a diminished fruit supply

to the monkeys in winter (Fig. 7.11). A similar case of resource unpredictability has been described for the *Rhinopithecus roxellana* population at the Zhouzhi Reserve: heavy snowfalls in spring 2001 destroyed vast amounts of flowers of plants, so that fruits became scarce in the following fall, and the monkeys were forced to shift to other plant parts [Li B et al. 2002b].

Fig. 7.11. *Sorbus* sp. fruits in the Samage Forest suffering from fungus attacks.

On an annual basis, mature leaves contributed only negligibly to the diet, but ingestion of deciduous mature leaves as well as deciduous and evergreen mature bamboo leaves was relatively high in the fall, accounting for a maximum of 19% in October when they were eaten along with fruit. In order to ensure a balanced nutrition, the high percentage of carbohydrate-rich fruit in the fall diet probably needed to be complemented with protein-rich leaves because a ripe-fruit-dominated diet would be incompatible with the pH level requirements to maintain microorganisms and cause fermentative acidosis [Kay and Davies 1994]. In general, mixing dietary items whenever possible is a means by which folivores reduce the impacts of toxins and digestion-inhibiting compounds (e.g. [Westoby 1978]).

Outside the fall, the snub-nosed monkeys did not feed much on mature leaves. In spring, they spent up to 93% of their feeding time consuming young foliage. Their strong preference for young leaves is likely due to the fact that young leaves are usually more digestible and generally contain more protein than mature ones ([Choo et al. 1981], but see

e.g. [Schülke et al. 2006]). Other vegetative matter such as flowers, bark and tubers were taken in low quantities.

Most of the ingested lichens have a pendulous appearance and belong to the filamentous fruticose ('alectorioid') lichens, the most notable ones being the light-colored *Usnea longissima* or long-beard lichen and the dark-colored *Bryoria* spp.. Roughly 90% of the lichens selected at our study site were of the genus *Usnea*. The trial experiments revealed a preference for *Usnea*. An ad lib observation of a male picking *Usnea* out of a bundle composed of both species in an *Abies georgei* tree lends further support to the notion that *Usnea* is favored over *Bryoria*. In striking contrast to our results, Kirkpatrick [1996] found that 92% of the picked lichens were of the genus *Bryoria*. He noted (p. 84) that "...*Usnea longissima* did not appear of interest to the langurs; when langurs were in trees holding both *Bryoria* and *Usnea longissima*, the langurs fed almost solely on *Bryoria*". This apparent contrast might perhaps be linked to the fact that *Usnea* is more abundant at moderate altitudes than *Bryoria* (Grueter, unpubl.) and the overall altitudinal range of our focal group at Samage is about 800 m lower than Wuyapiya. Alternatively, this geographical variation in food selection could also reflect cultural variation [Nishida et al. 1983; Zweifel and Bastian 2007]. It is also possible that there is a difference in the chemical properties of *Usnea* and *Bryoria* at the two sites.

As for sex difference in lichen eating, our results are incongruous. While DS15 indicates that males spent significantly more time feeding on lichens compared to females, no sex differences are apparent in DS30. Males are much larger in body size than females, and larger-bodied primates may be better able to subsist on a generalized (low-quality) staple fallback diet [Gaulin 1979; Haag 2007; Kay 1984]. Moreover, females have relatively greater energetic requirements as a result of gestation, lactation and infant carrying which may explain their tendency to feed on more (high-quality) non-lichen foods. However, empirical evidence supporting these assertions is ambiguous (e.g. [Doran et al. 2002; Strier 1991]).

Advantages of Lichen as a Fallback Food in Relation to Vascular Plants

Lichens are a symbiotic consortium of fungal and photosynthetic partners and thus do not represent a plant food in the classic sense. The winter dry season poses a nutritional challenge to the hardy snub-nosed monkeys; they are confronted with a lack of preferred plant resources and must choose between abundant lichen and abundant evergreen mature

foliage. Evergreen leaves in temperate forests are tough, leathery and chemically defended [Kirkpatrick 1996]. This low palatability thus makes them poor choices of food, so switching to mature leaves in winter is barely an option for the snub-nosed monkeys (but see [Curtin 1975] for *Semnopithecus schistaceus*).

Lichens are a non-seasonal resource and available in abundance. They are also relatively easy to harvest, requiring no extractive or technically difficult foraging capabilities (although the monkeys sometimes appeared to selectively pick the younger thinner strands out of a bundle of *Usnea*). A fallback strategy involving staple fallback foods is possibly cognitively less demanding than a filler fallback strategy whereby a primate is forced to switch to an otherwise neglected or rarely utilized resource base during the lean period (cf. [Russon and Begun 2004]).

The main predictors of colobine food choice are fiber content, protein and tannins. While tannins and fibers tend to have a negative effect on food choice in colobines, proteins have the reverse effect [Fashing et al. 2007a; Hanya et al. 2007; Oates et al. 1980; Waterman and Kool 1994]. *Rhinopithecus bieti* never or only extremely rarely or accidentally eat conifer needles [this study; Kirkpatrick 1998; Yang and Zhao 2001]. Gymnosperms have significantly higher loads of fiber and tannin than fruticose lichens [Kirkpatrick 1996]. Moreover, lichens contain virtually no fibrous components such as cellulose or lignin, making them highly digestible [Kirkpatrick 1996; Kirkpatrick et al. 2001]. They are also rich in non-structural carbohydrates which supply digestible energy for thermoregulation in winter (*ibid*.). These chemical differences may be a key reason why lichens have been chosen as a fallback instead of conifer foliage.

The crude protein content of fruticose lichens is generally low [Kirkpatrick 1996; Rominger et al. 1996], and for ungulates, it has been suggested that access to non-lichen forage in winter would be beneficial to counteract the protein deficit and potential rumen inhibition incurred from lichen eating [Rominger and Oldemeyer 1990]. *Rhinopithecus bieti* at Samage complement their winter diet with fruits and terrestrial herbs, and this dietary mix may confer more nutritional advantages than a purely lichen-based diet. Usually only leaves are regarded as being high in protein content, but recent studies have demonstrated that fruit may be equally important as sources of protein, even in temperate forests [Li 2006; Schülke et al. 2006]. However, specific phytochemical analyses are needed to determine the nutrient content of the particular fruits being of importance to the snub-nosed monkeys.

Fruticose lichens of the genera *Bryoria* and *Usnea* contain usnic acid acids, which have antibacterial properties and may hinder digestive processes in the (ungulate) rumen ([Brodo and Hawksworth 1977], cf. also [Lawrey 1986]). Non-lichen diet supplements may be vital to dilute lichen toxins, or higher-protein food may be required to stimulate microbial activity and enhance passage rates [Rominger and Oldemeyer 1990]. Some lichen taxa, e.g. *Sulcaria virens* are deemed toxic (Wang LS, pers. com.). Whenever *Sulcaria* grew along with *Usnea* on a tree, the snub-nosed monkeys in this study obviously singled out *Usnea* and did not handle *Sulcaria* at all (Fig. 7.12). *Sulcaria* was also totally avoided in opportunistic trial experiments, indicating an inherent or learned knowledge of which foodstuffs might be hazardous. With the exception of one study [Kirkpatrick et al. 2001], the physiological basis of lichen consumption in colobines has not been studied and warrants increased attention.

Fig. 7.12. Three lichen genera distributed in the Samage Forest: *Usnea longissima* (left), *Sulcaria* sp. (middle), and *Bryoria* sp. (right).

Lichens may also be essential as a source of free water during cold, dry and sunny climate conditions such as the ones being characteristic for the Himalaya foothills. Especially the dark-colored lichens in the genus *Bryoria* (common at high elevations within the habitat of *Rhinopithecus bieti*) are thought to be good absorbers of solar radiation, thus causing snow to melt and potentially making liquid available for the monkeys [Sharnoff and Rosentreter 1998].

Lichen Eating in Other Primates and Other Mammals Living in Temperate Habitats

For some primates, lichens are an occasional food item that is eaten in small quantities (e.g. *Colobus guereza* [Harris and Chapman 2007], *Cercopithecus lhoesti* [Kaplin and Moermond 2000], *Semnopithecus schistaceus* [Sayers and Norconk 2008], *Macaca fuscata* [Nakayama et al. 1999] and *Homo sapiens* [Wang 2004]). Habitual lichenivory, though, represents a specialization that among primates is largely restricted to the snub-nosed langurs (*Rhinopithecus bieti* [this study; Kirkpatrick 1996; Wu 1991]; *R. roxellana* [Li 2001]). Although fruticose lichens are found in various Afromontane habitats (e.g. Virunga Volcanoes [Owiunji et al. 2005], Simen Mountains [Iwamoto and Dunbar 1983]), their cercopithecoid and hominoids inhabitants such as *Gorilla beringei* and *Theropithecus gelada* do not seem to utilize this resource at all [Grüter and Zinner 2004; Watts 1984]. Two exceptions are the colobine *Colobus angolensis* in the montane Nyungwe National Park which ingests substantial amounts of lichen [Vedder and Fashing 2002] and *Macaca sylvanus* in Algerian oak forests which rely heavily on lichens during winter [Ménard 1985]. Among the Neotropical species, *Oreonax flavicauda* living in high-altitude habitats in Peru have been observed to incorporate yet unspecified amounts of lichens into their diet [Butchart et al. 1995].

Lichen-eating is also a fallback strategy in ruminants inhabiting temperate mountains and forests. Especially caribou (*Rangifer tarandus*) and black-tailed deer (*Odocoileus hemionus*) use arboreal lichen - including *Usnea* and relatives - for a fourth or more than a half of their winter diet [Richardson and Young 1977; Rominger and Oldemeyer 1990; Terry et al. 2000]. Musk deer (*Moschus* spp.) have also been reported to feed to a great extent on *Usnea* lichens [Green 1987; Ustinov 1969]. Lichens also constitute an important winter food for mountain goats (*Oreamnos americanus*) [Fox and Smith 1988] and North American moose (*Alces alces*) [Thomas 1990]. Among the non-ungulates, northern flying squirrels (*Glaucomys sabrinus*) depend largely on lichens in winter [Maser et al. 1986]. What becomes evident from this taxonomic summary is that the great majority of bulk feeders on lichens have a sacculated stomach.

Implications of Lichenivory for Social Organization and Structure

In theory, we would expect declining group sizes in more seasonal and marginal habitats as a result of declining productivity, i.e. smaller and fewer food patches [Plavcan et al. 2005; van Schaik and Brockman 2005]. Alternatively, foods in more seasonal areas are available in greater abundance (albeit of lower quality) and thus are not worth a fight and allow large groups to form (*ibid*.). Exploiting abundant or superabundant and evenly distributed resources on an annual basis reduces the ecological costs of long-term grouping and dampens feeding competition of the scramble type (*sensu* [Marshall and Wrangham 2007; Steenbeek and van Schaik 2001; van Schaik and van Noordwijk 1988; Wrangham 1979; Yeager and Kool 2000]). The cornucopia of lichen and the fact hat lichens are rarely if ever depleted in a patch at once (Grueter, pers. obs.) is evidence for weak competition and is thought to permit the formation and maintenance of 'super-groups' in snub-nosed monkeys [Kirkpatrick et al. 1998]. The cascading effects on social dynamics (competitive regime etc.) remains to be elucidated in detail, but spatially dispersed foods are hypothesized to generate weak or non-existent dominance hierarchies [Isbell 1991; van Schaik 1989; Wrangham 1980]. Snub-nosed monkeys still appear to experience competition to some degree when focusing on contestable and preferred plant foods such as *preferred* fruit items which create the foundation for competition (Chapter 8 in this thesis). This competition is likely enhanced during the lean season when fruits become increasingly scarce (cf. [van Schaik and Brockman 2005; Wrangham 1980]).

Moreover, it has also been proposed that lichens' slow regeneration time selects for the formation of large bands because aggregating in super-groups and collective foraging is a means of avoiding depleted patches of food [Kirkpatrick et al. 1998]. This hypothesis, the Cody-Altmann hypothesis [Rodman 1988], has thus far, however, rarely been invoked as a likely explanation of grouping in primates in general and its plausibility is seriously compromised due to its group selection argumentation [Harcourt and Stewart 2007]. Hence, we argue that lichenivory *allows* the creation of bands, but does not *induce* it.

In a striking socioecological parallel to the snub-nosed monkeys, two populations of montane-living *Colobus angolensis* show extensive consumption of lichens and live in extremely large groups of several hundred [Fashing et al. 2007b]. Lichen eating *C. angolensis* living in huge groups with 500+ animals have also been reported for the montane forests of Kahuzi-Biega (J. Yamagiwa, pers. com.). While the internal structure and functional basis of

these groupings remains unclear, lichens may at least play a role in facilitating the formation of super-groups in *C. angolensis* [Fashing et al. 2007b].

Implications for Three-dimensional Use of Space

If temperature was the primary determinant of altitude use, the snub-nosed monkeys would stay at the lowest altitudes in winter where temperature is higher. At Samage, it was found that they remain at moderately high altitudes in winter despite freezing winter nights. No significant difference in mean altitude of the group between fall and winter was detected [Chapter 4 in this thesis]. This unexpected result is best explained with dietary needs: lichen density is higher at higher elevations (this study), and lichen intake mitigates the negative effects of increased thermal stress associated with staying at high elevations.

Implications for Ranging and Foraging Strategies

According to standard foraging theory [Norberg 1977; Stephens and Krebs 1986], primates of the temperate zone facing food crunches during the winter bottleneck period basically have two options to maintain daily food intake: they may invest in traveling and thereby incurring higher energetic costs and caloric expenditure in order to acquire a sufficient quantity of the preferred foods (high-returns foods). Alternatively, they can modify their dietary spectrum by incorporating lesser-quality fallback foods, usually showing a concomitant decrease in moving. The first strategy, the 'high-returns strategy' is adopted by only a few temperate-living primates (e.g. [Bleisch 1995; Curtin 1975; Sayers and Norconk 2008]). The second strategy, the energy-saving strategy, appears to be the norm (e.g. [Ding and Zhao 2004; Guo et al. 2007; Mehlman 1986; Ménard and Vallet 1997; Nakagawa 1989; Xiang 2005a]). The particular tactic a given primate resorts to depends largely on whether prolific food items are available in winter. Since temperate biota are usually characterized by a virtual absence of profitable resources (with the exception of long-persisting winter fruits), a high-returns strategy is usually not an option.

Rhinopithecus bieti at Samage also feed on winter fruits. Tracking these diffusely distributed and energetically profitable fallback fruits might be the impetus for them to move out of their core area and visit peripheral patches of forest ('short-term habitat shifting') after fruit resources had been depleted in more central areas of the home range. These forays may

have caused them to keep a large home range in winter [Chapter 5 in this thesis]. On the other hand, they showed a decreased day journey length in winter as a consequence of cold temperatures (Grueter et al. unpubl.). With regard to optimal foraging models, the winter strategy pursued by *R. bieti* at Samage is a mixture of both: their subsistence on lichens as a fallback [this study; Ding and Zhao 2004; Kirkpatrick 1996] and reduced day journey length basically comply with the energy-minimizing strategy, but visiting peripheral areas in search of thinly dispersed fruit is consistent with the high-returns strategy.

Implications for Anatomy of the Masticatory Apparatus

Fallback foods have been hypothesized to be strong selective forces on morphology [Marshall and Wrangham 2007; Rosenberger 1992]. The relatively robust mandible of the Chinese rhinopiths as opposed to *Trachypithecus* and *Macaca* has probably evolved as a phenotypic adaptation to the tough staple fallback food available in their marginal arid temperate habitat [Pan et al. 2008]. Fruticose lichens most likely have fracture properties unlike those of young leaves or unripe fruits. In order to render the lichens' cell contents accessible to digestion, prolonged chewing and strong mastication force are probably necessary [Jablonski et al. 1998].

Implications for Conservation

Lichens are only sporadically collected by humans in the area as foods and fire kindling. However, dead standing trees are usually festooned with considerable amounts of lichen and are regularly climbed by the snub-nosed monkeys for the purpose of acquiring this resource ([this study], see also [Li 2006]), so the occasional removal of dead trees by villagers as a source of firewood has a negative impact on the lichen biomass.

The present results on lichen regeneration are preliminary in nature and based on a limited sample size, but together with the data provided by Kirkpatrick [1996], they tentatively signify that renewal rates are extremely slow and lichens need decades to recover from harvesting. Moreover, cursory inspection revealed that in areas through which the monkeys had recently passed, branches were not devoid of lichen. However, the snub-nosed monkeys live in a highly fragmented habitat and at some sites suffer from artificial range restricting as a means of attracting tourists, which increases their susceptibility to depletion

effects. Thus, depletion over the long-term may be a realistic scenario. Even though no quantitative data on the potential problem of lichen depletion are available for this site or any other inhabited by snub-nosed monkeys, it is reasonable to assume that continued lichen consumption or destruction exceeding annual production would result in a decreased standing crop.

Usnea longissima is the single most numerous food constituent in the diet of the snub-nosed monkeys at Samage. The abundance of this resource likely sets the carrying capacity of the community. That primate populations are limited by the availability of their key fallback resource has been empirically demonstrated (e.g. [Marshall and Leighton 2006]). The odds of the snub-nosed monkeys' survival are to a large degree dependent on the preservation of this critical resource. That habitat change or a decline of the major fallback food can cause local extinctions has been exemplified by the Amboseli *Cercopithecus aethiops* [Alberts et al. 2005]. As for *R. bieti*, it is alarming that exactly this species of lichen has been found to be vulnerable and susceptible to human-induced environmental changes, e.g. a dramatic decline in European forests has been attributed to air pollution in general and sulphur dioxide in particular [Esseen et al. 1981; Seaward 1987]. Lichens lack a protective cuticle and roots and thus absorb substances from the atmosphere via dry and wet deposition [Purvis et al. 2007].

China is the world's largest emitter of sulphur dioxide [Smith et al. 2001], and lichens are likely most at risk of deterioration in the industrialized and heavily polluted Eastern and Central areas of China. Nevertheless, it is conceivable that the Eastern Himalayas could still be affected, in the way that for example the Arctic is a sink for atmospheric pollution generated in the heavily industrialized north temperate regions [Klein and Vlasova 1992]. This would have a devastating and irreversible effect on the last remaining population of this highly endangered and charismatic primate. While hard data on lichen depletion and deterioration are not available for this area at the moment, this is an alarm signal that should be taken seriously and hopefully promotes more in-depth research in this field.

Choice of Fallback Foods and Foraging Strategies of Other Temperate-living Monkeys

Broadly speaking, different evolutionary lineages have developed different solutions to the problem of seasonal food scarcity. Phylogenetic constraints and resource availability

during the lean season are probably key determinants of the kinds of fallback foods that are utilized. Overall, buds and bark are the dominant fallback foods of temperate-living primates, followed by herbs (Fig. 7.13). With the single exception of fruit, fallback foods in temperate environments are to a large degree congruent with winter foods. Fruits emerge in the fall and often remain available long into winter. So winter fruits are often preferred and thus not fallback foods *sensu stricto*. Some colobines forage on winter fruits/seeds (e.g. [Guo et al. 2007; this study]), while this strategy is surprisingly uncommon among cercopithecines. On the other hand, mature leaves (including gymnosperm needles) act as fallback foods in macaques (e.g. [Mehlman 1988]), but are hardly of importance for temperate-living 'leaf monkeys'. Mature leaves are eaten as fallback foods by only a few temperate taxa, and unexpectedly, mature leaves were not an essential fallback food for colobines with the single exception of *Semnopithecus schistaceus* [Curtin 1975; Sayers and Norconk 2008]. For no single colobine species do mature leaves constitute the principal resource base in winter (Fig. 7.13). The stereotype of colobines as 'leaf monkeys' thus does not hold in this case. Apart from the foods listed in Fig. 7.13, crop raiding is another means by which monkeys buffer themselves from food shortages and is exhibited by some temperate monkeys (e.g. *Macaca mulatta* [Teas et al. 1980]).

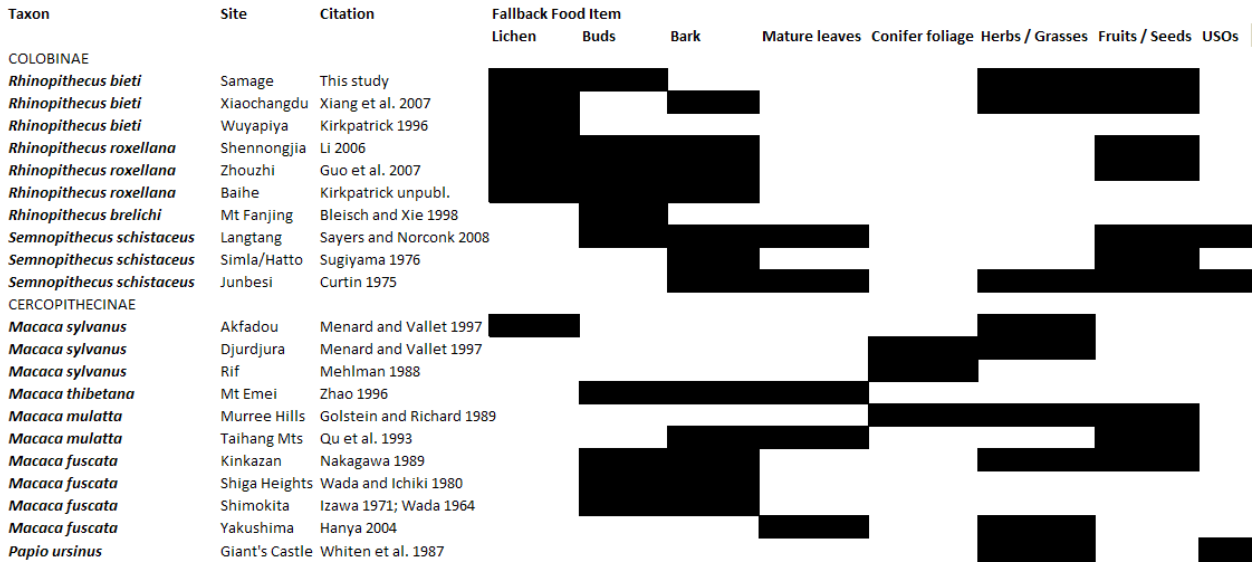


Fig. 7.13. A tabular overview of fallback foods in temperate Old World Monkeys. Two north temperate primate species are not included since no data on their respective dietary regime are available: *Macaca munzala* [Sinha et al. 2006] and *Trachypithecus geei* [Srivastava 2006; Wangchuk et al. 2003]. Among the south temperate primates, only the montane-living *Papio hamadryas* ursinus is included. 'Fruits/seeds' include acorns and pine nuts, 'herbs/grasses' include grass shoot bases. 'Yakushima' refers to the high-altitude sites only. The data were extracted from the following sources: [Curtin 1975; Goldstein and Richard 1989; Guo et al. 2007; Hanya 2004; Izawa 1971; Kirkpatrick 1996; Kirkpatrick and Gu 1999; Li 2006; Mehlman 1988; Ménard and Vallet 1997; Nakagawa 1989; Qu et al. 1993; Sayers and Norconk 2008; Sugiyama 1976; Wada 1964; Wada and Ichiki 1980; Whiten et al. 1987; Xiang et al. 2007a; Zhao 1996].

There are also examples of convergences in fallback strategies in distantly related taxa inhabiting ecologically similar habitats in different biogeographic regions. A case example are North African *Macaca sylvanus* populations and Central Asian *Rhinopitheus bieti* populations. Both incorporate considerable amounts of lichen in their diet in winter, despite divergent anatomy and physiology of the gastrointestinal tract (forestomach fermentation in snub-nosed monkeys and caeco-colic fermentation in macaques ([Lambert 1998]). With regard to the exploitation of conifer foliage, however, the two differ drastically: Barbary macaques in high altitude fir forests at the Ghomoran Rif show a clear feeding adaptation to the firs by being able to rely on fir foliage during the cold, snowy winters [Mehlman 1988] while no evidence of needle leaf feeding has been accrued in *R. bieti* (this study) despite the abundance of this particular resource in its habitat (early reports of needle eating (e.g. [Mu and Yang 1982]) have almost certainly been misinterpreted since no subsequent study has substantiated the initial records).

Fallback Strategies in Temperate-dwelling Hominins

Homo heidelbergensis was a partially and *H. neanderthalensis* an exclusively temperate-dwelling hominin taxon [Reed and Fish 2005]. As these hominins began to reside in cold habitats with enhanced seasonal climatic stress, meat became more important to the diet and they likely concentrated on obtaining meat via tactical hunting [Bocherens et al. 1999; Reed and Fish 2005; Roebroeks 2001]. Nevertheless, the low energetic value (in relation to suspected handling times) and the 'riskiness' of a foraging strategy involving hunting may have made meat an unlikely candidate for an essential fallback food ([Speth 1989], cf. [Mitani and Watts 2005; Wrangham et al. 1999]).

Conclusions

Snub-nosed monkeys (*Rhinopithecus bieti*) feed on lichens throughout the year, but the proportional representation of this item increased dramatically in winter when edible plant foods became rare. These primates are unique for having the capacity to rely to such a large extent on a single resource base during the long precarious winter. This high reliance on lichen is simply a consequence of the fact hat in their ecologically challenging environment there is a shortage of dietetically valuable vegetative matter, i.e. edible mature deciduous foliage (due to leaf shedding in the fall). It is probably reasonable to assume that in most of the habitats occupied by *R. bieti* there is no other fallback resource besides lichens that can provide the basis for their continued survival. An array of threats such as habitat disturbance, fragmentation, anthropogenic range restriction, slow regeneration time of lichen, depletion and environmental pollution seriously compromise viability of the remaining populations.

CHAPTER 8: *Rhinopithecus bieti* at Samage, China: Dietary Profile in Relation to Spatial Availability of Plant Resources and its Socioecological Implications

Introduction

Primate food habits are studied for a variety of reasons. Such studies may reveal a species' resource requirements [Litvaitis 2000], but diet-related factors such as nutritional quality, distribution and spatio-temporal fluctuations in abundance of food may also have far-reaching influences on the emergence of primate social organizations and social structure [Chapman 1990; van Schaik 1989; Wrangham 1980]. They may affect group size [Kirkpatrick 1996], tendency toward fission-fusion [Anderson et al. 2002] as well as the intensity and the nature of feeding competition (scramble vs. contest) [Janson and van Schaik 1988; Koenig et al. 1998; Saj and Sicotte 2007a; van Schaik and van Noordwijk 1988].

Non-human primates exhibit clear preferences for particular food items [Milton 1981]. Many factors - both internal and external - affect and mould patterns of food choice in primates, e.g. energy needs, nutrient requirements, constraints of the digestive system, body size, chemical and structural properties of foods and spatiotemporal availability of food resources [Barton and Whiten 1994; Garber 1987; Kay 1984; Lambert 2007; McKey et al. 1981; Milton 1984; Oates 1987; Oftedal 1991].

Colobines possess specialized capacious and partitioned stomachs [Caton 1998; Stevens 1988] where microbial fermentation of cellulose takes place [Bauchop and Martucci 1968; Hume 1989; Kay and Davies 1994; Kuhn 1964]. This enables them eat food containing high levels of structural polysaccharides (cellulose and related compounds) as found for instance in mature leaves that cannot be digested by primates lacking such forestomach fermentation. Overall, colobines can be classified as 'vegetarians', ingesting flowers, fruits, shoots, and seeds to varying degrees [Bennett and Davies 1994; Fashing 2007; Kirkpatrick 2007; Oates 1994]. The most frequent component in the diet is relatively easily digestible young leaves for some colobine populations [Boonratana 1993; Kool 1989; Werre 2000], mature leaves for others [Newton 1992], seeds or whole fruits for yet others [Davies 1991;

Dela 2007; Fashing 2001b; McKey et al. 1981], and lichens for a few [Kirkpatrick 1996]. Another common feature of colobine feeding ecology is their seasonally varying dietary spectrum as a response to temporal variation in food resource availability, of which switching to less nutritious plant foods (mature leaves) during periods of shortage of preferred food items is a key element [Dasilva 1994; Fashing 2001b; Struhsaker 1975]. While this is true for many tropical-dwelling colobines, some outliers within the Colobinae exemplify the group's great plasticity pertaining to environmental conditions and demonstrate that dietary strategy is only partly determined by evolutionary history (*sensu* [Struhsaker and Oates 1975]. A case in point are the black-and-white snub-nosed monkeys (*Rhinopithecus bieti*) of the temperate climate zone, which despite similar anatomy and presumably physiology, exhibit a somewhat deviating foraging strategy.

Previous work has revealed that black-and-white snub-nosed monkeys are highly dependent on lichen [Kirkpatrick 1996; Xiang et al. 2007a], thus being the only simian primate whose main food is not a plant. Their dietary regime has been shown to vary geographically and to depend on overall habitat condition and productivity: in high latitude/high altitude habitats, lichens constitute the major fraction of the diet in virtually every month and are complemented with leaves from dicots and monocots [Kirkpatrick 1996; Xiang et al. 2007a]. The natural environment of *R. bieti* is characterized by striking seasonal variation in food resource availability. Winter is a period of plant food deprivation, and an almost exclusive dependence on carbohydrate-rich lichens has been regarded as a key ecological adaptation [Kirkpatrick 1996; Xiang et al. 2007a; Chapter 7 in this thesis]. Groups associated with more productive habitats at lower elevations and latitudes have a more diversified diet and include a substantial proportion of non-lichen foods on a seasonal basis, such as immature leaves, fruits/seeds, buds, flowers, bamboo shoots, and bark of various plants [Ding and Zhao 2004; Yang and Zhao 2001].

So far, there have been only two published studies on dietary profile and strategy of *R. bieti* so far [Ding and Zhao 2004; Xiang et al. 2007a]. This chapter has the objective of documenting the overall dietary spectrum of a previously unstudied population and providing a thorough assessment of habitat composition. These findings are important for comprehending the species' resource requirements and the carrying capacity of the habitat and thus have implications for conservation management. A companion paper [Chapter 7 in this thesis] deals with fallback strategies, seasonality in food use and lichenivory and their consequences for socioecology and conservation.

For colobines, the question how diet affects socioecology has been discussed especially in relation to the importance of scramble and also contest competition. Scramble competition is defined as the collective exhaustion of limited resources leading to lower foraging efficiency for all group members [Janson and van Schaik 1988]. Scramble competition increases as groups increase in size and is thought to limit group size. As a result of a more rapid depletion of food patches, larger groups are forced to travel farther to ensure procurement of a sufficient amount of the food [Chapman and Chapman 2000; Janson and van Schaik 1988; Majolo et al. 2008; van Schaik and van Noordwijk 1988]. Scramble competition is usually inferred to exist if there is a positive association between group size and home range size or day range. Based on weak relationships between these variables in combination with small group sizes and ubiquity of food resources, folivorous or frugivorous-folivorous primates such as colobines have traditionally been viewed as experiencing only a low intensity of within-group scramble competition [Fashing 2001a; Isbell 1991; Janson and Goldsmith 1995; Steenbeek and van Schaik 2001; Sterck et al. 1997; Yeager and Kirkpatrick 1998; Yeager and Kool 2000]. However, group size effects have recently been demonstrated among various folivores [Gillespie and Chapman 2001; Koenig et al. 2008; Majolo et al. 2008; Saj and Sicotte 2007b; Snaith and Chapman 2008; Teichroeb et al. 2003].

This study of a colobine living in very large groups may help resolve this issue. We assess the degree to which the lichenivorous-folivorous-frugivorous dietary regime of this colobine species generates the potential of scramble and also contest competition. We use the following observations as indicators of food competition: 1) Preferred food species (species with high selection ratios) occur at low densities across the home range and are spatially clumped and thus can probably not accommodate all band members (*between-unit contest*) (cf. [Koenig et al. 1998]). 2) Valued patches of food are being depleted (*within-band contest*) (cf. [Snaith and Chapman 2005]). 3) Unit members avoid co-feeding (*within-unit scramble* or *contest*) [Saj and Sicotte 2007b] by having fewer nearest neighbors when feeding as compared to resting (assuming that dispersion reduces competition (cf. [van Schaik and van Noordwijk 1988].

Methods

Study Site

I conducted the present study in the predominantly temperate Samage Forest near the village of Gehuaqing (27°34'N, 99°17'E) in Yunnan's Baimaxueshan National Nature Reserve. The study area is approximately bounded by Samage Mountain (4100 m) in the West, Dayalu Cliffs in the East, the villages of Gehuaqing, Digong and Lamasi (all within Weixi County) in the south and the village of Nidima (Deqin County) in the north. Xiangguqing to the east lies beyond the boundaries of the home range of this group. Narrow valleys and steep hillsides characterize the topography at Samage. Land cover at the research area is a mosaic of mixed coniferous and deciduous-broadleaf forest (at 2900-3600 m), sub-alpine George's fir forest (3500-4000 m), montane sclerophyllous oak forests (3200-3500 m), subtropical evergreen broadleaf forest (2500-3000 m), Yunnan pine forest (2500-3100 m), as well as cattle pastures at various elevations. Umbrella bamboos (*Fargesia* spp.) and rhododendra form an important element of the underbush in all vegetation types. Parts of the Samage Forest have been selectively logged, and anthropogenic disturbance in the form of livestock grazing and collection of NTFP (non timber forest products) is widespread. An extensive trail system allows access to most corners of the study area. The habitat of the monkeys at this locality ranges from 2500 m to 4000 m and includes all major vegetation types, with mixed forest being the most used ecotype and clearcuts being unsuitable habitat for *R. bieti*. The semihabituated focal group is composed of ca. 410 members.

Climate

Annual rainfall was 1004 mm, and mean annual temperature was 14.3°C at 2448 m (800 m below the altitude the study group most frequently visited). Distribution of precipitation was highly irregular, and temperature varied strikingly with seasons: there was a steep increase in rainfall from spring onwards and a prolonged winter drought season with freezing nights (for details on climate, see Chapters 4 and 7 in this thesis). Complete snow cover rarely lasted for more than a few days within the frequently used zone of the group as snow fall was followed by prolonged sunny days.

Data Collection

I collected data on diet composition over 20 months between Sep 2005 and July 2007. Scan records were obtained on 116 days. The rugged terrain with steep-sided ravines and impenetrable undergrowth (bamboo etc.) made tracking difficult, and thus distance observations from prominent topographical features (rocks etc.) with help of a spotting scope were the methods of choice. Adverse weather (monsoon rains and prevailing mist in summer, snowfalls and very strong winds in winter) and obstructive vegetation sometimes caused me to terminate recording sessions despite the animals still being in the vicinity. Occasionally I also engaged in observations of the group at close range.

Scans of all visible animals were taken at 15 min or 30 min intervals. If a large number of monkeys were in view, I chose 30 min scans; if only a small number was visible, I did 15 min scans. Scans needed to be completed at least 5 min before the beginning of the next scan. Every scan included information on date, time and weather conditions. For every subject being scanned, I recorded age, sex, activity (for definitions, see Appendix to Chapter 3), as well as distance to nearest neighbor and identity of nearest neighbor. I strove to get scan data spread evenly throughout the day. Age/sex classes are divided into the following categories: adult male, adult female, juvenile (ca 1-4 yr old), subadult male, infant (<1 yr). The category 'SAMOF' (subadult male or female) is useful for cases where it was not possible to determine the sex of an animal whose body size is close to or bigger than that of an adult female, but was not accompanied by an infant (cf. [Bleisch et al. 1993]).

Scan records of feeding behavior also included the food item, plant part and its age as well as plant species whenever possible. The following foods were distinguished: lichens (fruticose vs. foliose), young leaves (including spring buds/shoots), mature leaves, buds (dormant leaf buds), flowers, flower buds, bark, pith, fruit (both ripe and unripe), seeds, invertebrates, snow, fungi, water, bamboo shoots, and tuber. It was usually difficult to see whether the small fruits were eaten wholly or whether the flesh was discarded. If I was unable to identify the tree taxon by eye, I attempted to collect some samples from that feeding tree or a nearby tree of the same taxon for later identification. When the animals fed on buds or young sprouts in spring, I marked the feeding tree whenever possible and gathered a sample a few months later when the tree bore fruits, flowers and/or mature leaves.

During forest walks outside scan sessions, I recorded all partially consumed and discarded foods on the forest floor with tooth marks or other signs of having been handled by the monkeys. I used evidence from such feeding sign as a complementary measure to

estimate seasonal variance in diet composition. Observational sampling was usually biased toward arboreal feeding, so the importance of terrestrial foods such as bamboo shoots was likely underrepresented.

The composition of the forest was investigated via stratified random sampling, i.e. we subdivided the forest into five distinct forest types or strata [Mueller-Dombois and Ellenberg 1974]. The different strata are described fully in Chapter 4 in this thesis. Li Dayong, the field assistants and I established a total of 67 plots of 20 m x 20 m each (area: 26'800 m^2). Allocation of plots to the available strata was based on the proportional availability of different vegetation types within the central part of the study area [Krebs 1999]. We determined the availability of strata through reconnaissance surveys and a GIS (geographic information system) vegetation map. Within each stratum, we placed plots with an objective of sampling at different altitudinal belts (200 m intervals). Within these belts, we laid out plots along existing trails using a random walk procedure, whereby we drew a random number (100-999) and then located a sample plot by taking this number of paces at 500 m intervals.

We only included trees with girth over 40 cm. We recorded the following physical dimensions for all trees in the plots: tree height, crown diameter, bole height and girth. Girth was measured using a forestry tape, and later converted to diameter at breast height (DBH). Tree density per plot was converted to number of trees per hectare. Basal area per tree is the cross-sectional area of a tree at breast height and was calculated by the following formula:

$$BA = [.5 * DBH]2 * \pi$$

We identified tree specimens in plots (n = 1851) *in situ* to species or genus level using reference books [Raven and Wu 1994-2005; Unknown 1972]. If *in situ* identification was not feasible, we collected voucher specimens which were inspected by staff of the Alpine Botanical Garden in Shangri-La, Yunnan.

On a monthly basis, we recorded presence/absence of fruits, flowers and young leaves for 157 food trees and calculated the percentage of trees bearing each of the phenophases every month. For details on phenology monitoring, see Chapter 5 in this thesis.

Data Analysis

An indication of the degree to which primates are selective in their choice of food tree species can be obtained by calculating a selection index [Krebs 1999]. This compares the proportion of feeding observations of a plant species with the relative abundance of the species concerned as estimated from the tree plots. Basal area is used to express the relative species crown biomass and potential food abundance, and the selection index is calculated from the formula:

$$W_i = O_i/P_i$$

where W_i is the selection index, O_i the percentage of feeding observations for species *i*, and P_i the percentage of total basal area accounted for by species *i*. $W_i > 1$ indicates preference, $W_i < 1$ avoidance.

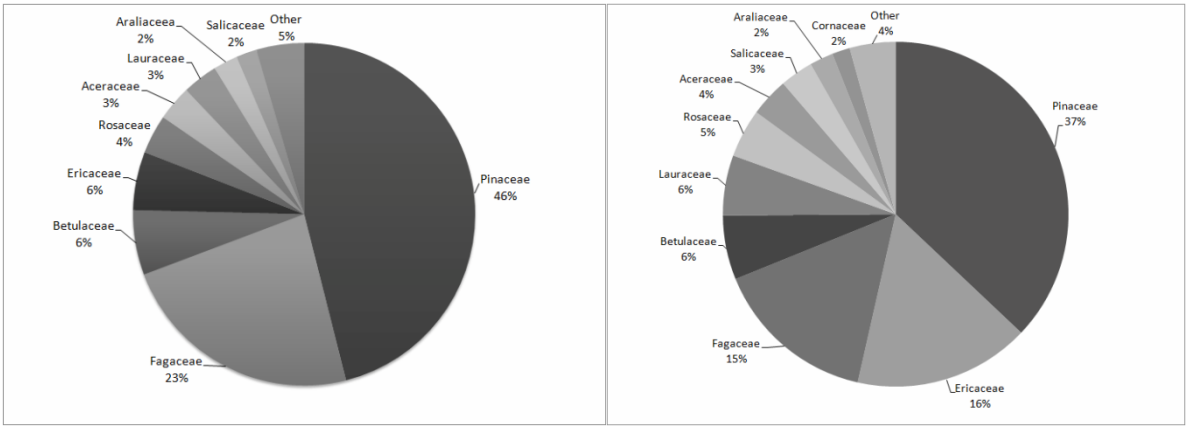
Using tree data obtained from the plots, I measured the pattern of dispersion of important food tree species. I used the coefficient of dispersion (CD) (cf. [Koenig et al. 1998]). The CD refers to the ratio of the variance to the mean of the number of species in a sample. If species were distributed randomly, their allocation in the sample would correspond to a Poisson distribution (mean equals variance; CD = 1). CD > 1 indicates a clumped/contagious distribution, a CD < 1 a uniform distribution. I determined significant departures from randomness (i.e. departure from a variance-to-mean ratio of 1.0) using the chi-square statistic [Brower et al. 1998; Perry and Mead 1979].

Results

Forest Composition

We recorded a total of 80 tree species of 23 families in the botanical plots (Fig. 8.1; Tab. 8.1). An additional 9 species of rare woody plants – *Bretschneidera sinensis* (Bretschneideraceae), *Magnolia campbellii* (Magnoliaceae), *Corylus chinensis* (Betulaceae), *Populus yunnanensis* (Salicaceae), *Meliosma yunnanensis* (Sabiaceae), *Cerasus conadenia* (Rosaceae), *Clethra delavayi* (Clethraceae), *Ilex delavayi* (Aquifoliaceae), and *Rhododendron sinogrande* (Ericaceae) - were not represented in the plots. The family Pinaceae contributed the greatest

biomass at Samage based on both basal area and stem density. The two top families together, viz. Pinaceae and Fagaceae, accounted for 69 % of the total basal area. The three top families together, viz. Pinaceae, Ericaceae and Fagaceae, accounted for 75% of the total basal area and 69% of the total stem density. As estimated by basal area, the three dominant tree species at Samage are *Abies georgei*, *Cyclobalanopsis* cf. *gambleana* and *Picea likiangensis*. 35% of the tree species are evergreen, 65 % deciduous. Of the conifers (*n* = 10 species), 10 % are deciduous (*Larix*), of the broadleaf trees, 27% evergreen.



(a) (b)

Fig. 8.1. The most common plant families at the Samage Forest, Baimaxueshan Nature Reserve. (a) Based on basal area, (b) based on no. of stems (*n* = 1898).

Tab. 8.1. The 20 most common tree species at the Samage Forest based on basal area.

Rank	Species	Family	Basal area/ha [cm^2/ha]	% total biomass
1	*Abies georgei*	Pinaceae	84734	13.3
2	*Cyclobalanopsis* cf. *gambleana*	Fagaceae	83359	13.0
3	*Picea likiangensis*	Pinaceae	80014	12.5
4	*Pinus yunnanensis*	Pinaceae	57869	9.0
5	*Tsuga dumosa*	Pinaceae	41230	6.4
6	*Quercus pannosa*	Fagaceae	37128	5.8
7	*Abies ernestii*	Pinaceae	23294	3.6
8	*Rhododendron rubiginosum*	Ericaceae	18651	2.9
9	*Quercus rehderiana*	Fagaceae	18185	2.8
10	*Alnus nepalensis*	Betulaceae	15389	2.4
11	*Acanthopanax evodiaefolius*	Araliaceae	14724	2.3
12	*Betula utilis*	Betulaceae	14644	2.3
13	*Machilus microcarpa*	Lauraceae	14333	2.2
14	*Acer laxiflorum*	Aceraceae	10015	1.6
15	*Corylus* cf. *wangii*	Betulaceae	8802	1.4
16	*Sorbus* cf. *thibetica*	Rosaceae	8245	1.3
17	*Quercus aliena*	Fagaceae	8094	1.3
18	*Taxus yunnanensis*	Taxaceae	7315	1.1
19	*Tilia chinensis*	Tiliaceae	6288	1.0
20	*Cornus macrophylla*	Cornaceae	6166	1.0

Diet Repertoire

Around 150 different vegetative food items from at least 94 species and 38 families contributed to the diet of *R. bieti* at Samage. Foraging took place both on the ground and in the canopy. Food items were obtained from 40 woody plant species (49% of all available tree species), 22 shrubs, 1 semi-parasitic shrub, 7 vines, 2 root-parasitic herbs, and 14 species of terrestrial herbaceous vegetation (THV). Food lists are presented in Tabs. 8.2 and 8.3. In terms of stem density, food trees (excluding species supporting lichen only) accounted for 30.4% (n = 40 species) of the trees in the study area. In terms of relative dominance, the basal area of food trees comprised 35% of the total basal area in the study area. The top 10 food tree species (Tab. 8.4) accounted for >90% of the total feeding time on plant foods. All top 10 food tree species had selection ratios higher than 1, with a few species having extraordinarily high selection indices, i.e. *Pterocarya delavayi* (82.1; represented by a single specimen in the plots), *Padus obtusata* (40.0) and *Acanthopanax evodiaefolius* (22.3) (Tab. 8.4). Many species listed in Tab. 8.2 were fed on infrequently. As evinced by feeding records,

immature leaves of *Acanthopanax evodiaefolius* were the single most prominent food type (Tab. 8.5). As evinced by feeding remains, shoots of *Fargesia* spp. were the most important dietary item (Tabs. 8.6, 8.7). The average number of plant species and specific plant food items used per month was 16 and 19, respectively. The diversity of food species was highest in April with 32 species and 38 items and October with 34 species and 38 items (Fig. 8.2).

Tab. 8.2. Food repertoire of *R. bieti* at Samage: vascular plants. The list is based on systematic scan observations, opportunistic observations and food remnants.

Predominant life form	Species	Part	Month
	ANGIOSPERMS		
	FAGACEAE		
Tree	*Quercus aliena*	Shoot	Apr
Tree	*Quercus pannosa*	Seed	Sep
		Flower	Jul
Tree	*Cyclobalanopsis* cf. *gambleana*	Seed	Jan
		Pith	Apr
	JUGLANDACEAE		
Tree	*Pterocarya delavayi*	Young leaf	Apr
	ACERACEAE		
Tree	*Acer* sp.	Bud	Feb
Tree	*Acer* sp.	Seed	Sep
Tree	*Acer laxiflorum* var. *laxiflorum*	Young leaf	Apr, May
		Petiole	May
		Flower	May
Tree	*Acer mono* var. *macropterum*	Young leaf	Apr
Tree	*Acer caesium*	Young leaf	Apr
Tree	*Acer hookeri*	Young leaf	Apr
Tree	*Acer caudatum*	Flower bud	May
		Young leaf	May
	BRETSCHNEIDERACEAE		
Tree	*Bretschneidera sinensis*	Petiole	Oct
		Seed	Sep
	ARALIACEAE		
Tree	*Acanthopanax evodiaefolius*	Mature leaf	Jul, Aug, Sep, Oct
		Young leaf	Apr, May, Jun
		Flower bud	Feb, Apr
		Fruit	Aug, Sep, Oct, Nov, Jan, Feb
		Bark	Mar, May, Sep
		Bud	Jan, Feb, Mar, Dec
		Petiole	Jun, Jul
Shrub	*Acanthopanax leucorrhizus* var. *fulvescens*	Leaf	Oct
	CELASTRACEAE		
Tree	*Euonymus theifolius*	Seed	Oct
	HYDRANGEACEAE		
Tree	*Hydrangea heteromalla*	Mature leaf	Jul, Sep, Oct, Nov
		Pith	Jul
Tree	*Hydrangea* sp.	Mature leaf	Aug

Tree	*Hydrangea* sp.	Bark	Jan
Tree	*Philadelphus delavayi* var. *delavayi*	Mature leaf	Oct, Sep, Aug
		Bark	Mar
Shrub	*Philadelphus* sp.	Young leaf	May
Shrub	*Deutzia glomeruliflora*	Mature leaf	Jul, Nov
		Young leaf	May
		Flower	May
	CLETHRACEAE		
Tree	*Clethra delavayi*	Petiole	May
		Young leaf	May
	CORNACEAE		
Shrub	*Helwingia japonica*	Mature leaf	Sep
Tree	*Cornus macrophylla*	Fruit	Aug, Sep
		Young leaf	Apr
	ROSACEAE		
Tree	*Sorbus rufopilosa*	Mature leaf	Jul, Oct
		Fruit	Aug, Sep
Tree	*Sorbus rehderiana* var. *cupreonitens*	Young leaf	May
Tree	*Sorbus* sp.	Young leaf	Jun
Tree	*Sorbus* sp.	Bud	Feb
Tree	*Sorbus oligodonta*	Young leaf	Apr
		Mature leaf	Oct, Nov
		Fruit	Aug, Oct, Nov
Tree	*Sorbus monbeigii*	Mature leaf	Jul, Sep
Tree	*Sorbus hupehensis*	Young leaf	Apr
Tree	*Sorbus macrantha*	Mature leaf	Oct
		Fruit	Jan, Oct
Tree	*Sorbus thibetica*	Bud	Feb
		Young leaf	Apr, May, Jun
		Fruit	Aug, Sep, Oct, Nov
		Flower, flower bud	Apr, May
Tree	*Sorbus epidendron*	Fruit	Feb
Shrub	*Stranvaesia davidiana*	Mature leaf	Mar, Apr, Dec
		Fruit	Oct
Tree	*Padus obtusata*	Fruit	Jun, Oct
		Young leaf	Apr, May, Jun
		Mature leaf	Jul, Oct
		Bud	Feb
		Flower bud	May
Tree	*Malus yunnanensis*	Young leaf	Apr, May
Tree	*Malus* cf. *prattii*	Fruit	Sep
Shrub	*Rosa macrophylla*	Seed	Oct
Shrub	*Rubus alexeterius*	Fruit	Jul
Tree	*Cerasus conadenia*	Mature leaf	Oct
Tree	*Cerasus patentipila*	Flower bud	May
		Young leaf	May
Tree	*Cerasus clarofolia*	Young leaf	Apr
		Flower bud	Apr
	CAPRIFOLIACEAE		
Shrub	*Lonicera tangutica*	Mature leaf	Oct
Vine	*Lonicera acuminata*	Mature leaf, fruit	Mar
Shrub	*Viburnum betulifolium*	Fruit	Feb, Oct
Shrub	*Viburnum nervosum*	Young leaf	May
Tree	*Viburnum cylindricum*	Fruit	Oct

Herb	*Sambucus adnata*	Fruit	Sep
Shrub	*Leycesteria formosa*	Mature leaf	Aug
	BALANOPHORACEAE		
Root-parasitic herb	*Balanophora involucrata*	Tuber	Oct
	LILIACEAE		
Shrub	*Polygonatum cirrhifolium*	Mature leaf	Aug
Herb	*Maianthemum atropurpureum*	Leaf	May
Herb	*Maianthemum forrestii*	All	Jun
	BERBERIDACEAE		
Shrub	*Berberis* sp.	Young leaf	Apr
	RANUNCULACEAE		
Vine	*Clematis obtusidentata*	Mature leaf	Oct
Vine	*Clematis chrysocoma*	Mature leaf	May
Herb	*Thalictrum delavayi*	Leaf	Oct
	OROBANCHACEAE		
Root-parasitic herb	*Boschniakia himalaica*	Tuber	Nov
	BALSAMINACEAE		
Herb	*Impatiens arguta*	Leaf	Oct
Herb	*Impatiens xanthocephala*	Leaf	Oct
	URTICACEAE		
Herb	*Urtica* sp.	Leaf	Oct
Herb	*Pilea angulata*	Leaf	May, Oct, Nov
Herb	*Elatostema obtusum*	Leaf	Nov
	CRUCIFERAE		
Herb	*Cardamine macrophylla* var. *macrophylla*	Leaf	Nov
Herb	*Eutrema yunnanense*	Leaf	Nov
	SCHISANDRACEAE		
Vine	*Schisandra rubriflora*	Fruit	Nov
		Young leaf	May
	GRAMINEAE		
Shrub	*Fargesia* cf. *dura*	Leaf	Feb, Mar, Sep, Oct, Nov
		Shoot	Jun, Aug
Shrub	*Fargesia* cf. *melanostachys*	Young leaf	Mar, Apr, May
		Mature leaf	Jul, Nov, Dec
		Shoot	May, Jun, Jul
Shrub	*Fargesia* sp.	Mature leaf	Jan, Aug
Shrub	*Yushania* sp.	Mature leaf	Oct
	TILIACEAE		
Tree	*Tilia chinensis*	Mature leaf	Oct
		Young leaf	Apr
	SALICACEAE		
Tree	*Salix rehderiana*	Young leaf	Apr
		Catkin	Mar, Apr
Tree	*Populus davidiana*	Young leaf	Apr
		Flower bud	Mar
		Bud	Mar
		Bark	Feb, Oct
	BETULACEAE		
Tree	*Betula utilis*	Young leaf	May
Tree	Unid. species	Young leaf	Apr
Tree	*Corylus ferox*	Young leaf	Apr
	LAURACEAE		
Tree	*Machilus yunnanensis*	Bud	Mar
		Mature leaf	Apr, Sep

Tree	*Machilus microcarpa*	Seed	Sep
Tree	*Litsea chunii*	Young leaf	Apr, May
		Flower	Apr
	OLEACEAE		
Shrub	*Ligustrum* cf. *delavayanum*	Fruit	Oct
Tree	*Syringa yunnanensis*	Mature leaf	Aug
	LEGUMINOSAE		
Shrub	*Piptanthus nepalensis*	Fruit	Sep
	COMPOSITAE		
Herb	*Senecio scandens*	Leaf	Oct
Herb	*Ligularia nelumbifolia*	Leaf	Aug
	ERICACEAE		
Tree	*Rhododendron rubiginosum*	Flower	May
Shrub	*Rhododendron yunnanense*	Young leaf	May, Jun
	Rhododendron selense	Petiole	May
Tree	*Enkianthus* cf. *deflexus*	Young leaf	Apr
Shrub	*Enkianthus chinensis*	Flower	Apr
Shrub	*Lyonia villosa*	Young leaf	Apr
	LORANTHACEAE		
Semi-parasitic shrub	*Arceuthobium pini*	All	Oct
	LARDIZABALACEAE		
Vine	*Holboellia angustifolia*	Mature leaf	Apr
Shrub	*Decaisnea fargesii*	Fruit	Aug
	ACTINIDIACEAE		
Vine	*Actinidia pilosula*	Young leaf	Apr
		Fruit	Oct
	VITACEAE		
Vine	*Cayratia* cf. *cardiospermoides*	Fruit	Oct
	SABIACEAE		
Tree	*Meliosma yunnanensis*	Fruit, mature leaf	Oct
	SAXIFRAGACEAE		
Herb	*Chrysoplenium davidianum*	All	
	AQUIFOLIACEAE		
Tree	*Ilex* sp.	Mature leaf	Jan, Feb, Apr, Nov, Dec
		Flower	Dec
		Young leaf	Feb
Tree	*Ilex delavayi*	Mature leaf	Jul, Aug
		Bark	Jan
	GYMNOSPERMS		
	CUPRESSACEAE		
Tree	*Sabina squamata*	Fruit	Mar
	PINACEAE		
Tree	*Larix speciosa*	Petiole	Apr, May, Jul, Sep

Tab. 8.3. Food repertoire of *R. bieti* at Samage: cryptogams, i.e. non-vascular plants (lichens) and fungi. The list is based on systematic scan observations, opportunistic observations and food remnants.

Species	Season
LICHENS	
PARMELIACEAE[1]	
Usnea longissima	Year-round
Usnea sp.	Year-round
Bryoria confusa	Year-round
Bryoria cf. *trichodes* cf. ssp. *americana*	Year-round
Cetrelia sp.	Apr, Dec
1 unk species	Nov
FUNGI	
Russulaceae	
Russula sp. 1	Jul, Aug, Sep, Oct
Russula sp. 2	Sep
Russula sp. 3	Aug
Russula senecis	Sep
Amanitaceae	
Amanita hemibapha var. *ochracea*	Aug
Amanita fritillaria	Sep
Amanita flavipes	Sep
Gomphaceae	
Gomphus floccosus	Aug, Sep
Boletaceae	
Boletus sp.	Aug, Sep

[1] The species of lichens have previously been reported in Chapter 7 in this thesis.

Tab. 8.4. Number of feeding records for the 10 top-ranked identified plant species.

Rank	Species	Family	No. feeding records	Selection index
1	*Acanthopanax evodiaefolius*	Araliaceae	437	22.3
2	*Sorbus* spp.[2]	Rosaceae	142	10.6
3	*Acer* spp.[3]	Aceraceae	72	2.7
4	*Sorbus* cf. *thibetica*	Rosaceae	59	5.4
5	*Fargesia* spp.[4]	Gramineae	51	NA[1]
6	*Pterocarya delavayi*	Juglandaceae	42	82.1
7	*Cornus macrophylla*	Cornaceae	17	2.1
8	*Padus obtusata*	Rosaceae	14	41.0
9	*Tilia* cf. *chinensis*	Tiliaceae	11	1.3
10	*Litsea chunii*	Lauraceae	8	7.2

[1] Shrub.

[2] Includes *Sorbus oligodonta*, *S. rufopilosa*, *S. rehderiana*, *S. monbeigii*, *S. hupehensis*, and *S. macrantha*; distinguishing among these species was difficult.

[3] Includes *Acer laxiflorum*, *A. mono*. *A. hookeri*, *A. caesium*, and *A. caudatum*; distinguishing among these species was difficult.

[4] Includes *Fargesia* cf. *melanostachys* and *F.* cf. *dura*. Identifying bamboos to species level was not possible.

Tab. 8.5. Number of feeding records for the 10 top-ranked specific food items.

Rank	Item	Family	No. feeding records
1	*Acanthopanax evodiaefolius* (YOUNG LEAF)	Araliaceae	207
2	*Acanthopanax evodiaefolius* (FRUIT)	Araliaceae	174
3	*Sorbus* spp.[1] (FRUIT)	Rosaceae	107
4	*Acer* spp.[2] (YOUNG LEAF)	Aceraceae	63
5	*Fargesia* spp.[3] (MATURE LEAF)	Gramineae	49
6	*Pterocarya delavayi* (YOUNG LEAF)	Juglandaceae	42
7	*Acanthopanax evodiaefolius* (BUD)	Araliaceae	40
8	*Sorbus* cf. *thibetica* (YOUNG LEAF)	Rosaceae	35
9	*Sorbus* cf. *thibetica* (FRUIT)	Rosaceae	19
10	*Cornus macrophylla* (FRUIT)	Cornaceae	17

[1] Includes *Sorbus oligodonta*, *S. rufopilosa*, *S. rehderiana*, *S. monbeigii*, *S. hupehensis*, and *S. macrantha*; distinguishing among these species was difficult.

[2] Includes *Acer laxiflorum*, *A. mono*. *A. hookeri*, *A. caesium*, and *A. caudatum*; distinguishing among these species was difficult.

[3] Includes *Fargesia* cf. *melanostachys* and *F*. cf. *dura*. Identifying bamboos to species level was not possible.

Tab. 8.6. The 10 top-ranked plant species, as evidenced from feeding traces.

Rank	Species	Family	Score
1	*Fargesia* spp.	Gramineae	104
2	*Acanthopanax evodiaefolius*	Araliaceae	71
3	*Sorbus* cf. *thibetica*	Rosaceae	23
4	*Sorbus* spp.[1]	Rosaceae	20
5	*Cornus macrophylla*	Cornaceae	11
6	*Cyclobalanopsis* cf. *gambleana*	Fagaceae	4
7	*Pterocarya delavayi*	Juglandaceae	3
8	*Padus obtusata*	Rosaceae	3
9	*Ilex* sp.	Aquifoliaceae	3
10	*Bretschneidera sinensis*	Bretschneideraceae	2

[1] Includes *Sorbus oligodonta*, *S. rufopilosa*, *S. rehderiana*, *S. monbeigii*, *S. hupehensis*, and *S. macrantha*; distinguishing among these species was difficult.

Tab. 8.7. The 10 top-ranked specific food items, as evidenced from feeding traces.

Rank	Item	Family	Score
1	*Fargesia* spp.[1] (SHOOT)	Gramineae	104
2	*Acanthopanax evodiaefolius* (FRUIT)	Araliaceae	49
3	*Sorbus* cf. *thibetica* (FRUIT)	Rosaceae	18
4	*Sorbus* spp.[2] (FRUIT)	Rosaceae	17
5	*Acanthopanax evodiaefolius* (MATURE LEAF)	Araliaceae	15
6	*Cornus macrophylla* (FRUIT)	Cornaceae	11
7	*Acanthopanax evodiaefolius* (YOUNG LEAF)	Araliaceae	7
8	*Sorbus* cf. *thibetica* (YOUNG LEAF)	Rosaceae	5
9	*Cyclobalanopsis* cf. *gambleana* (PITH)	Fagaceae	4
10	*Ilex* sp. (MATURE LEAF)	Aquifoliaceae	3

[1] Includes *Fargesia* cf. *melanostachys* and *F*. cf. *dura*. Identifying bamboos to species level was not possible.

[2] Includes *Sorbus oligodonta*, *S. rufopilosa*, *S. rehderiana*, *S. monbeigii*, *S. hupehensis*, and *S. macrantha*; distinguishing among these species was difficult.

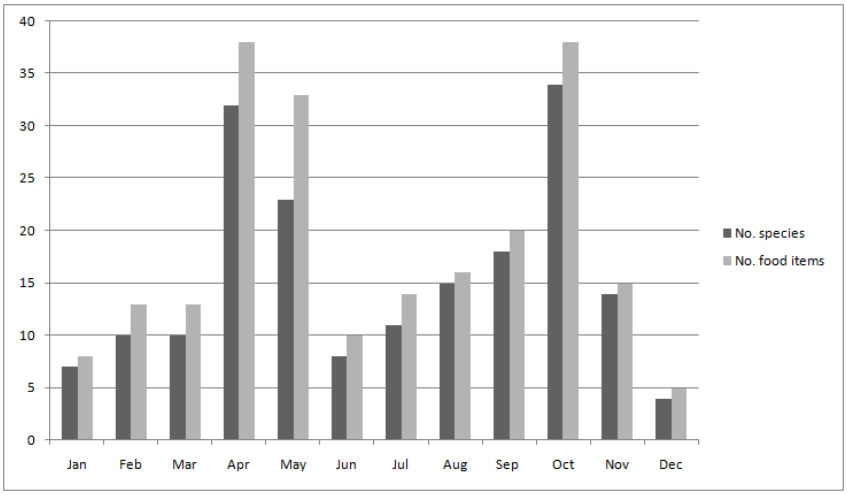


Fig. 8.2. Food species diversity of *R. bieti* at Samage compared among months.

Most of the frequently taken fruits were usually ingested wholly. The small size of most fruits, e.g. the pome *Sorbus* and the drupes *Acanthopanax* and *Cornus*, made extraction of seeds probably uneconomical. A percentage of the seeds may pass through the digestive tract intact. Seeds were extracted and fruit flesh discarded only in a few species, e.g. *Euonymus theifolius* (Fig. 8.3). *Acanthopanax* and *Sorbus* fruits were usually picked off directly with the teeth without involvement of the hands. The monkeys consumed both mature and immature fruits of the top food species.

Mature leaves were chosen and ingested from both deciduous and evergreen trees, but only a few woody species were important sources of mature leaves, i.e. the deciduous

Philadelphus delavayi, *Sorbus* spp., *Acanthopanax evodiaefolius* and the evergreen *Ilex* sp.. For some species, only petioles were eaten (e.g. *Bretschneidera sinensis*), for others only the leaf blades (e.g. *Stranvaesia davidiana*) and for yet others both leaf blades and petioles (e.g. *Acanthopanax evodiaefolius*).

Fig. 8.3. Seeds of *Euonymus theifolius* were extracted from the pericarp by *R. bieti* at Samage.

The snub-nosed monkeys fed on subterranean parts of *Boschniakia himalaica* and *Balanophora involucrata*. They spent a considerable amount of time unearthing unidentified tubers (hidden food items). I observed juveniles and females eating snow in winter, but only on rare occasions. The monkeys drank water from small ponds and streams. Contrary to Xiang et al. [2007a], the monkeys of this population were never observed to eat resin. We recorded a case of predation on bird eggs. One individual was seen feeding on the flesh of an unidentified flying squirrel (Sciuridae). I observed them biting into mushrooms in the fall. I also saw them removing the bark of dead fallen and standing trees (mostly *Abies georgei*) and disassembling rotten and brittle tree stumps. While I never clearly saw an individual actually eating an insect, these latter observations may indicate foraging on invertebrates. Feeding on bamboo (*Fargesia* spp.) leaves was witnessed in all seasons. Bamboo shoots (*Fargesia* spp.) were consumed in large quantities in summer.

Food Competition

I tested the prediction that preferred food trees have a low density within the home range and are spatially clumped. While the overall density of trees was 708 stems per ha, the three main food trees comprised only 42.5 individuals per ha (6.0%) (Tab. 8.8). The single most important woody food species *Acanthopanax evodiaefolius* was found in only 16.4% of the vegetation plots. All top three food tree taxa - *Acanthopanax evodiaefolius*, *Sorbus thibetica* and *Sorbus* spp. - showed a clumped distribution.

Tab. 8.8. Density and dispersion of major food of *R. bieti* at Samage. ** designates a significant deviation from randomness ($p < 0.05$). Numbers in parentheses refer to the 35 plots in mixed forest only.

Species	*n*	Density (ha^{-1})	% Plots[2]	Index of dispersion (variance-to-mean-ratio)	Distribution	Mean/plot (if n > 0)
Acanthopanax evodiaefolius	41	15.3	16.4 (31.4)	5.2 ** (4.7**)	Contagious	3.7
Sorbus thibetica	16	6.0	17.9 (28.6)	1.4 ** (1.3)	Contagious[3]	1.3
Sorbus spp.[1]	57	21.3	26.9 (48.6)	3.8** (3.1**)	Contagious	3.1
A. evodiaefolius, *S. thibetica* & *Sorbus* spp.	114	42.5	40.3 (68.6)	5.7** (4.5**)	Contagious	4.2
All	1898	708.2				

[1] Includes *Sorbus oligodonta*, *S. rufopilosa*, *S. rehderiana*, *S. monbeigii*, *S. hupehensis*, and *S. macrantha*; these species were lumped together for the analyses because distinguishing among them *in situ* was not straightforward.

[2] Percentage of plots with species *i*.

[4] Random in mixed forest.

In order to assess whether valued patches of food were being exhausted, I use opportunistic evidence of patch depletion. On several occasions, I encountered evergreen trees that were completely defoliated after the *R. bieti* group had visited them (Tab. 8.9). Especially the leaves of *Ilex* and *Philadelphus* were highly sought after (Fig. 8.4).

Tab. 8.9. Ad lib observations of broadleaf trees having been depleted through intense foraging by *R. bieti*.

Species	No. of depleted trees and dates	BA (%)
Philadelphus delavayi	5 (Oct 05), 2 (Nov 05), 5 (Aug 06), 2 (Oct 06), 2 (Nov 06)	0.08
Ilex sp.	2 (Oct 05), 1 (Jan 07)	0.03
Ilex delavayi	3 (Oct 05), 3 (Nov 05), 1 (Feb 06), 1 (Mar 06), 2 (Aug 06), 2 (Oct 06), 4 (Nov 06)	0[1]
Hydrangea heteromalla	1 (Jul 07)	0.03
Malus yunnanensis	1 (May 07)	0.09

[1] Not recorded in plots.

Fig. 8.4. A *Philadelphus* tree that has been stripped off all the foliage after the group of *R. bieti* had passed through.

To verify if unit members avoid co-feeding, I checked whether one-male unit (OMU) members have fewer nearest neighbors when feeding as compared to resting. When an OMU member was feeding (n = 5020; excluding bachelors and infants), in only 4.6% of all records was there another member in proximity (0-2 arm's lengths). When an animal was resting, in 41.5% of all records did it have another member within proximity.

Discussion

In Chapter 7 in this thesis, I have shown that lichens represent the staple food of *R. bieti* at Samage: lichens were chosen perennially and comprised ca 67% of all the feeding records. Lichens were complemented with plant material (12% young leaves, 11% fruits, 4% mature leaves). Seasonal feeding patterns on plant items exactly matched the temporal variation in

the availability of the main plant phenophases. The monkeys exploited immature leaves prolifically in spring and ingested heavy quantities of fruit in summer and fall. In the present chapter, I have demonstrated that the dietary diversity of this population encompasses 94 different plant species and a few unusual items (mammal, mushrooms, bamboo). Moreover, I have shown that plant species were not consumed in accordance with their spatial abundance, but that the monkeys showed a strong preference for uncommon species with a clumped distribution and that - based on several lines of evidence - they may be subjected to scramble and contest competition to a certain degree.

Dietary Peculiarities

Detritus found in the group‘s foraging path indicates that bamboo shoots constitute a highly important summer food for *R. bieti* at Samage. Extensive use of bamboo (shoots and leaves) is an uncommon strategy in primates, restricted to those Old World Monkey species living in central-south Asian and central-east Africa in montane forests, viz. Tibetan macaques (*Macaca thibetana* [Zhao 1996]), Himalayan langurs (*Semnopithecus schistaceus* [Sayers and Norconk 2008]), ‘golden monkeys’ (*Cercopithecus mitis kandti* [Twinomugisha et al. 2006]), mountain gorillas (*Gorilla beringei beringei* [Vedder 1984]), and bamboo lemurs (*Hapalemur* spp. [Tan 1999]).

Mycophagy *sensu stricto* (excluding lichen) is a common dietary strategy only in Goeldi’s monkeys (*Callimico goeldii* [Hanson et al. 2003]), but otherwise an occasional strategy for a few temperate and tropical primates, e.g. Japanese macaques (*Macaca fuscata* [Wada and Ichiki 1980]), green monkeys (*Chlorocebus sabaeus* [Harrison 1984]), bonobos (*Pan paniscus* Bermejo et al. 1994]), *Rhinopithecus roxellana* [Kirkpatrick and Gu 1999]. Judging from the bite marks, *R. bieti* at Samage often did not eat the whole fungus, but left a substantial portion untouched. This may be related to the supposition that some fungi cause gastrointestinal distress (e.g. *Gomphus floccosus*).

Acorn feeding was observed only once in this study; this low rate of occurrence is surprising given that other studies highlight the preponderance of acorn in the diet of both *R. bieti* [Xiang et al. 2007a; Zhong et al. 1998] and *R. roxellana* [Tan et al. 2007]. Low visibility at Samage may impede detectability of foraging for acorns in leaf litter on the forest floor.

Feeding on *vertebrate matter* is most unusual among colobines. There is one published case of a male grey leaf monkey (*Presbytis hosei*) raiding the nest of a babbler and eating the eggs and perhaps one young hatchling [Goodman 1989]. *R. bieti* seem to be partly

faunivorous, as demonstrated by records of cannibalism [Xiang and Grueter 2007] and the here presented incident of ingestion of flesh from a mammal.

Digging up *USOs* (*underground storage organs*) - as demonstrated in this study - is a form of extractive foraging [Sayers 2008]. Feeding on bamboo shoots also requires a certain amount of manipulative skill: the monkeys break off the shoots with their hand, discard the sheaths with teeth before eating the juicy center.

Plant Food Selection and Diversity

75% of the woody stems at Samage are Pinaceae (pines, firs, hemlocks and spruces), Fagaceae (oaks) and Ericaceae (rhododendrons), none of which are of direct dietary importance to the snub-nosed monkeys (cf. [Kirkpatrick 1996]). Conifers and oaks are, however, important lichen-loading trees and almost exclusively exploited for this non-plant resource [Chapter 7 in this thesis]. *R. bieti* at Samage derived its plant diet mostly from the deciduous angiosperms families Araliaceae, Rosaceae, Aceraceae, Juglandaceae and Cornaceae. High selection ratios for most of these angiosperm plant species indicate strong selectivity for uncommon species. That plant material was acquired from uncommon trees suggests that there are constraints on the choice of species, which likely due to variability in nutritional quality.

Only a few fruit species provided the majority of the diet in summer and fall, viz. *Acanthopanax evodiaefolius*, *Sorbus* spp., *Sorbus* cf. *thibetica*, and *Cornus macrophylla*. Of *Sorbus* and *Acanthopanax*, the monkeys ate both fruits and mature leaves at the same time, often in an alternating fashion.

Mature leaves contributed relatively marginally to the diet of *R. bieti* at Samage [Chapter 7 in this thesis]. Most of the ingested mature leaves (most notably *Acanthopanax evodiaefolius*, *Sorbus* spp., *Padus obtusata, Hydrangea heteromalla, Philadelphus delavayi, Fargesia* spp., and *Ilex* spp.) were deciduous with the exception of *Ilex* spp. and *Fargesia* sp. In line with our results, Sayers and Norconk [2008] demonstrated for Himalayan langurs a preference for broad-leaved deciduous mature leaves to evergreen mature leaves. In general, *R. bieti* at Samage displayed a preference for young over mature leaves [Chapter 7 in this thesis]. Compared to mature foliage, young foliage generally has higher nutritional quality (higher in protein, lower in fiber and secondary compounds) [Boonratana 1993; McKey et al. 1981; Milton 1979; Oates et al. 1980].

The diversity of plant species consumed was highest in April, May (the leafing season) and October (the fruiting season) when preferred items were most abundant. This is in general agreement with other studies on *R. bieti* [Ding and Zhao 2004; Xiang et al. 2007a], but in contrast to some studies on other colobines which demonstrated decreased dietary diversity when favorite foods were abundant (e.g. [Bennett 1983; Yeager 1989a]).

Intra and Inter-specific Differences

There has been some discrepancy with regard to the feeding strategy of *R. bieti*. Kirkpatrick [1996] stressed the species' relatively monotonous dependence on lichens (specialists strategy) whereas Ding and Zhao [2004] accentuated its dietary diversity (generalists strategy). As it has turned out, this inconsistency is likely a consequence of different habitat characteristics. *R. bieti* populations occur in different ecological conditions, and findings from the Wuyapiya population, which inhabits one extreme of *R. bieti* habitat [Kirkpatrick 1996], are not representative of all other populations. In a gradient from south to north, precipitation and temperature decrease while average altitude increases and the vegetation becomes progressively poorer. The limited diet of the Wuyapiya and also Xiaochangdu population [Xiang et al. 2007a] in the north is a consequence of low species diversity. The Samage forest is floristically richer and more productive compared to Xiaochangdu and Wuyapiya and foraging options are thus less constrained. This study confirms that the dietary spectrum and key foods largely hinge on the particular habitat, climate condition and botanical composition and diversity. The number of species consumed clearly decrease with increasing altitude and latitude. At the northern end of the species' geographical range (Wuyapiya and Xiaochangdu), they consumed 20 and 25 plant species in 12 and 13 months, respectively [Kirkpatrick 1996; Xiang et al. 2007a]. In the central part of the species' range (Tacheng-Xiagguqing and Samage-Gehuaqing), they fed upon 50 (excluding lichens) and 94 species during 14 and 20 months of study, respectively [Ding and Zhao 2004; this study]. At the southern end (Longma), they incorporated an assumed 97 species into the diet [Huo 2005]. Dietary breadth of the Samage and Longma populations is comparable to most tropical sites where Asian colobines have been studied (e.g. [Curtin 1980; Davies 1991; Kool 1993]).

The top ranking dietary genus of *R. bieti* at Samage was *Acanthopanax* (alternatively named *Eleutherococcus*), of which the monkeys consumed all major phytophases, viz. young leaves in spring, mature leaves summer and fall, fruit in summer, fall and winter, buds in

winter and bark all year round. *Acanthopanax* was not part of the diet of *R. bieti* at Wuyapiya and Xiaochangdu, probably due to the genus' low density there [Kirkpatrick 1996], but it is harvested by *R. bieti* populations living to the south of Samage [Liu et al. 2004]. The closely related allopatric and ecologically comparable *Rhinopithecus roxellana* has a similar diet, both in terms of food plant genera and species [Guo et al. 2007; Li 2006]. Among the non-*Rhinopithecus* taxa, Himalayan langurs of Nepal are of great comparative value due to their association with biogeographically, botanically and topographically similar habitats. While *Acanthopanax* is a key food plant species for *R. bieti*, Himalayan langurs did not include *Acanthopanax* at all into the diet despite the genus being relatively common there [Sayers and Norconk 2008]. On the other hand, the shrub *Gaultheria* was eaten in considerable quantities by Himalayan langurs, and despite being superabundant at Samage, evidence for inclusion in the diet of 'Himalayan snub-nosed monkeys' is lacking.

What do these Data tell us About the Possibility of Food Competition?

Snaith and Chapman [2007] review several lines of evidence that are indicative of food competition in colobines and other 'folivorous' primates. We have previously shown a positive correlation between group size and home range size for different populations of *R. bieti*, indicating scramble competition effects (productivity also had some effect on home range size) [Chapter 5 in this thesis]. Given the fact that lichens occur in profusion in their natural habitat (at least currently), *R. bieti* are thought to be free to form large groups and food competition would not be expected to be prevalent [Kirkpatrick et al. 1998; Chapter 7 in this thesis]. A different picture emerges when considering non-lichen, i.e. plant resources, which are the focus of this paper.

With this study, I demonstrated for this species and population that preferred food trees are spatially clumped and occur at low densities across the home range and are possibly not large enough to accommodate a fairly cohesive 400-member band at the same time. These distributional features are all indicative of contest competition [Koenig et al. 1998; van Schaik 1989; but see Isbell et al. 1998; Koenig and Borries 2006]. That preferred plant parts such as young foliage show a restricted temporal availability [Chapter 7 in this thesis] provide further support for the existence of competition. Food quality has not been addressed so far.

Some comparatively rare and highly preferred (and supposedly high-quality) plant resource patches, e.g. leaves of *Ilex* and *Philadelphus*, became exhausted after the group of *R.*

bieti had encountered them. Along the same lines, Kirkpatrick [1996] notes that at least three *Sorbus* trees were defoliated in the path of the *R. bieti* band. *Ilex* spp. (holly) and *Philadelphus delavayi* (mock orange) occurred at very low stem densities, and also in terms of basal area, they all accounted for only 0.15% of the total basal area of all trees. These opportunistic data indicate that *R. bieti* undeniably deplete some plant resources.

It has been proposed that an efficient way to alleviate the costs of food competition is to avoid co-feeding [Saj and Sicotte 2007b; Siex and Struhsaker 1999; van Noordwijk and van Schaik 1987], i.e. spreading out while feeding and consequently having fewer nearest neighbors while feeding as compared to resting. My results confirm that feeding individuals had fewer conspecifics in proximity than resting ones. However, I have never seen a female behaving competitively toward other female unit members while feeding in a patch or supplanting another female from a food source.

While competition *within* units was more of the scramble type, the low density and clumped distribution of preferred resources are suggestive of *between*-unit contest competition (note that within/between-*unit* competition is different from within/between-*group* competition, as described in the socioecological model). I have previously shown that male aggressive behavior is positively correlated with temporal availability of fruit (Chapter 3 in this thesis) and that the only recorded band fission event happened in late winter when valued fruit resources became rare and extremely patchy (Chapters 3 and 5 in this thesis). Some ad lib observations substantiate the possibility of contest competition among units: in May 2006, large dominant OMUs appeared to defend leafing trees (rare *Pterocarya* trees) from other nearby units. The lower ranking units appeared to wait in nearby conifer trees eating lichens until the more dominant units left the leafing trees. In Jan 2007, one unit was seen chasing away another unit from an *Acanthopanax* tree that still bore fruits. These observations recall Isbell's [1991] proposition that species that feed on both dispersed and clumped resources might reduce competition by shifting from clumped to dispersed foods. Competition among OMUs for access to food trees has also been reported for *R. roxellana* [Zhang et al. 2003]. Male and female black-and-white colobus monkeys (*Colobus polykomos*) that depend on fruit for some part of their diet have also been seen participating in food defense [Korstjens 2001].

While still preliminary, my results demonstrate that the pervasiveness of food competition might have a constraining effect upon the species' socioecology. Specifically, this should limit group size, but it does not. So there must be an advantage of forming large

groups that counteracts the disadvantage associated with feeding competition, such as threats stemming from nearby roaming all-male units [Chapters 1 and 3 in this thesis].

Conservation Implications of the Diet Selection Study

Pointing out essential food resources of an endangered taxon such as *R. bieti* and assessing whether dietary preferences are narrow or whether there is ecological flexibility associated with diet are crucial for survival assessment. Incorporation of feeding ecology data should be an integral part of any environmental impact assessment plan. Whenever some sort of habitat alteration or wildlife management is planned, feeding ecology data have the potential to predict a population's response to such actions, and harmful effects can be mitigated if key resources have been identified and are left unharmed [Caro 1998; Clemmons and Buchholz 1997; Litvaitis 2000]. There exist plans to establish a local breeding colony of *R. bieti*, and data on relative diet composition are of vital importance for successful *ex situ* management [Lambert 2007].

We have previously demonstrated that *R. bieti* at Samage exhibits an overriding preference for mixed deciduous broadleaf and conifer forest over other forest types (Chapter 4 in this thesis). The present results substantiate that preferred food tree species are mostly deciduous angiosperms such as *Acanthopanax* that are located within this ecotype, which should be the major target of conservation efforts. Some deciduous trees offering seasonally valuable foods have been decimated locally, e.g. *Pterocarya delavayi*, and - given their high importance as food resources - should receive strict protection. Human activities encroaching upon the monkeys' food resources and thereby bringing about a decreased yield should be controlled more rigorously. Potential sources of competition are goats/sheep foraging on acorns in winter, and villagers scouring the forest for mushrooms and bamboo shoots.

Conclusion and Areas for Future Research

Due to earlier observations suggesting *R. bieti* to strictly feed on lichens, this species has originally been characterized as being one of the most dietetically specialized of all primates. Subsequent studies including mine have uphold that lichens are indeed a key dietary component, but also underpinned the dietary elasticity in response to variation in availability, abundance and diversity of plant food supply. *R. bieti* at Samage exhibit a rather

broad usage of the resources in their habitat (more than 90 plant species) and thus can be viewed as generalists. However, the dominant evergreen plant families did not offer many palatable foodstuffs to the monkeys so that they had to rely heavily on a few rather uncommon deciduous hardwood species. Some highly sought food trees occurred at (very) low densities and were irregularly distributed in space and time which are preconditions for the emergence of contest competition. In line with recent studies (references in Introduction), this study provides supporting evidence that feeding competition may be more widespread among colobines than previously thought. Future studies should aim to get a better understanding of food competition in this species, for instance by gathering data on patch residence time, patch size and unit size to evaluate patch depletion, a measurable behavioral indicator of the presence or absence of within group scramble competition [Snaith and Chapman 2005].

A salient finding of this study is that some mature leaves were totally avoided by *R. bieti* whereas others were highly sought after. It is widely known that protein content and fiber have a strong influence on leaf choice in colobines (e.g. [Davies et al. 1988; Fashing et al. 2007a; Oates et al. 1980; Waterman and Choo 1981]). Future research should investigate the phytochemical components associated with preferred and avoided food items, thereby contributing to a fuller comprehension of the feeding ecology of *R. bieti*.

Appendix

Appendix 1: Basal area of all trees in the botanical plots in the Samage Forest

Rank	Species	Family	Basal area/ha [cm^2/ha]	% total biomass	Life form[1]
1	*Abies georgei*	Pinaceae	84734	13.25	C
2	*Cyclobalanopsis* cf. *gambleana*	Fagaceae	83359	13.04	E
3	*Picea likiangensis*	Pinaceae	80014	12.51	C
4	*Pinus yunnanensis*	Pinaceae	57869	9.05	C
5	*Tsuga dumosa*	Pinaceae	41230	6.45	C
6	*Quercus pannosa*	Fagaceae	37128	5.81	E
7	*Abies ernestii*	Pinaceae	23294	3.64	E
8	*Rhododendron rubiginosum*	Ericaceae	18651	2.92	E
9	*Quercus rehderiana*	Fagaceae	18619	2.91	E
10	*Alnus nepalensis*	Betulaceae	15389	2.41	D
11	*Acanthopanax evodiaefolius*	Araliaceae	14724	2.30	D
12	*Betula utilis*	Betulaceae	14644	2.29	D
13	*Machilus microcarpa*	Lauraceae	14333	2.24	E
14	*Acer laxiflorum*	Aceraceae	10015	1.57	D
15	*Corylus* cf. *wangii*	Betulaceae	8802	1.38	D
16	*Sorbus* cf. *thibetica*	Rosaceae	8245	1.29	D
17	*Quercus aliena*	Fagaceae	8094	1.27	D
18	*Taxus yunnanensis*	Taxaceae	7315	1.14	C
19	*Tilia chinensis*	Tiliaceae	6288	0.98	D
20	*Cornus macrophylla*	Cornaceae	6166	0.96	D
21	*Acer* sp.	Aceraceae	4675	0.73	D
22	*Salix phanera*	Salicaceae	4472	0.70	D
23	*Salix rehderiana*	Salicaceae	4440	0.69	D
24	*Lindera kariensis*	Lauraceae	3976	0.62	D
25	*Rhododendron lukiangense*	Ericaceae	3832	0.60	E
26	*Sabina squamata*	Cupressaceae	3780	0.59	C
27	*Pinus armandii*	Pinaceae	3708	0.58	C
28	*Larix potaninii*	Pinaceae	3389	0.53	C (D)
29	*Sorbus vilmorinii*	Rosaceae	3100	0.48	D
30	*Rhododendron uvariifolium*	Ericaceae	3092	0.48	E
31	*Rhododendron yunnanense*	Ericaceae	2770	0.43	(D)[2]
32	*Populus davidiana*	Salicaceae	2732	0.43	D
33	*Sorbus monbeigii*	Rosaceae	2479	0.39	D
34	*Acer caudatum*	Aceraceae	2309	0.36	D
35	*Sorbus hupehensis*	Rosaceae	2190	0.34	D
36	*Rhododendron decorum*	Ericaceae	1916	0.30	E

37	*Machilus yunnanensis*	Lauraceae	1786	0.28	E
38	*Rhododendron fulvum*	Ericaceae	1624	0.25	E
39	*Cerasus clarofolia*	Rosaceae	1505	0.24	D
40	*Malus* sp.	Rosaceae	1259	0.20	D
41	*Sorbus epidendron*	Rosaceae	1223	0.19	D
42	*Acer caesium*	Aceraceae	1216	0.19	D
43	*Rhododendron anthosphaerum*	Ericaceae	1151	0.18	E
44	*Sorbus rufopilosa*	Rosaceae	995	0.16	D
45	*Rhododendron vernicosum*	Ericaceae	981	0.15	E
46	*Eurya cavinervis*	Theaceae	907	0.14	E
47	*Acer hookeri*	Aceraceae	864	0.14	D
48	*Litsea chunii*	Lauraceae	820	0.13	D
49	*Acer longipes*	Aceraceae	780	0.12	D
50	*Salix* sp.	Salicaceae	761	0.12	D
51	*Enkianthus deflexus*	Ericaceae	728	0.11	D
52	*Syringa yunnanensis*	Oleaceae	690	0.11	D
53	*Euonymus theifolius*	Celastraceae	640	0.10	E
54	*Acer mono*	Aceraceae	597	0.09	D
55	*Malus yunnanensis*	Rosaceae	589	0.09	D
56	*Viburnum glomeratum*	Caprifoliaceae	572	0.09	D
57	*Philadelphus delavayi*	Hydrangeaceae	504	0.08	D
58	*Sorbus* sp.	Rosaceae	496	0.08	D
59	*Tetracentron sinense*	Tetracentraceae	479	0.07	D
60	*Lyonia villosa*	Ericaceae	476	0.07	D
61	*Acer oliverianum*	Aceraceae	474	0.07	D
62	*Sabina pingii*	Cupressaceae	408	0.06	E
63	*Sorbus oligodonta*	Rosaceae	407	0.06	D
64	*Pterocarya delavayi*	Juglandaceae	400	0.06	D
65	*Acer heptalobum*	Aceraceae	393	0.06	D
66	*Sorbus* cf. *hemsleyi*	Rosaceae	385	0.06	D
67	*Lindera obtusiloba*	Lauraceae	351	0.05	D
68	*Ilex dipyrena*	Aquifoliaceae	288	0.04	E
69	*Padus perulata*	Rosaceae	283	0.04	D
70	*Macrocarpium chinense*	Cornaceae	253	0.04	D
71	*Padus obtusata*	Rosaceae	230	0.04	D
72	*Ilex* sp.	Aquifoliaceae	223	0.03	E
73	*Hydrangea heteromalla*	Hydrangeaceae	219	0.03	D
74	*Corylus ferox*	Betulaceae	204	0.03	D
75	*Toxicodendron vernicifluum*	Anacardiaceae	166	0.03	D
76	*Cerasus* sp.	Rosaceae	97	0.02	D
77	*Aralia chinensis*	Araliaceae	66	0.01	D
78	*Meliosma cuneifolia*	Sabiaceae	52	0.01	D
79	*Schima argentea*	Theaceae	50	0.01	E
80	*Viburnum cylindricum*	Caprifoliaceae	48	0.01	E

[1] E = evergreen broadleaf, C = conifer, D = deciduous.

[2] Semideciduous.

Appendix 2: Potential food items of Rhinopithecus bieti at Samage

The items listed here were assumed to have been manipulated by *R. bieti*, but ingestion is uncertain.

Predominant life form	Species	Part	Season
	ANGIOSPERMS		
	Compositae		
Herb	*Ainsliaea latifolia*	Leaf	
Herb	*Petasites tricholobus*	Flower	
Herb	*Cacalia palmatisecta*	Leaf	
	ARALIACEAE		
Herb	*Panax japonicus*	Fruit	Fall
Shrub	*Schefflera* sp.	Fruit	Fall
	LORANTHACEAE		
Semi-parasitic shrub	*Taxillus* cf. *delavayi*	Fruit, leaf	Summer
	ERICACEAE		
Shrub	*Gaultheria forrestii*	Fruit	Summer
Tree	*Rhododendron rubiginosum*	Pith	Spring
Tree	*Rhododendron* sp.	Bud	Winter
	ASTERACEAE		
Herb	*Megacodon stylophorus*	Leaf	
	PINACEAE		
Tree	*Picea likiangensis*	Bud	Winter
Tree	*Tsuga dumosa*	Flower	Spring
Tree	*Larix speciosa*	Bark	Fall
	GROSSULARIACEAE		
Shrub	*Ribes takare*	Leaf	Summer
	LAURACEAE		
Tree	*Machilus yunnanensis*	Flower bud	Winter
Tree	*Lindera obtusiloba*	Fruit	Summer
	Lindera kariensis var. *glabrescens*	Pith	
	ROSACEAE		
Tree	*Malus yunnanensis*	Mature leaf	Fall
Tree	*Sorbus oligodonta*	Flower	Fall
Tree	*Sorbus pteridophylla*	Mature leaf	Fall
Tree	*Cerasus clarofolia*	Fruit	Fall
Tree	**ACERACEAE**		
Tree	*Acer* cf. *fulvescens*	Mature leaf	Fall
	SALICACEAE		
Tree	*Populus davidiana*	Bark	Fall
Tree	*Salix* cf. *delavayana*	Bud	Fall
	LILIACEAE		
Herb	*Tupistra aurantiaca*	Leaf	Spring
		Fruit	Spring
Herb	*Trillium tschonoskii*	Leaf	Spring
	FAGACEAE		
Tree	*Quercus aliena*	Flower, flower bud	Spring
		Seed	Fall
	LEGUMINOSAE		
Shrub	*Piptanthus nepalensis*	Mature leaf	Fall
	OXALIDACEAE		
Herb	*Oxalis* sp.	Leaf	

	CORNACEAE		
Tree	*Macrocarpium chinense*	Flower	Spring
	HYPERICACEAE		
Shrub	*Hypericum patulum*	Leaf	Spring
	CAPRIFOLIACEAE		
Shrub	*Viburnum sympodiale*	Fruit	Summer
	POLYGONACEAE		
Herb	*Polygonum suffultum*	Leaf	Spring
	CRUCIFERAE		
Herb	*Cardamine griffithii*	All	Summer
	GYMNOSPERMS		
	CUPRESSACEAE		
Tree	*Sabina pingii*	Fruit	Summer
	FUNGI		
	Cortinarius sp.		Fall
	Hericium erinaceum		Fall

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